

# A STOCHASTIC MODEL FOR SPECIATION BY MATING PREFERENCES

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**ABSTRACT.** Mechanisms leading to speciation are a major focus in evolutionary biology. In this paper, we present and study a stochastic model of population where individuals, with type  $a$  or  $A$ , are equivalent from ecological, demographical and spatial points of view, and differ only by their mating preference: two individuals with the same genotype have a higher probability to produce a viable offspring. The population is subdivided in several patches and individuals may migrate between them. We show that mating preferences by themselves, even if they are very small, are enough to entail reproductive isolation between patches, and we provide the time needed for this isolation to occur. Our results rely on a fine study of the stochastic process and of its deterministic limit in large population, which is given by a system of coupled nonlinear differential equations. Besides, we propose several generalisations of our model, and prove that our findings are robust for those generalisations.

*Keywords:* birth and death process with competition, mating preference, reproductive isolation, dynamical systems.

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## INTRODUCTION

Understanding mechanisms underlying speciation remains a central question in evolutionary biology. The main puzzle is the origin of isolating barriers that prevent gene flow among populations. Ecological speciation has been largely studied, highlighting the relations between sexual selection and speciation, and demonstrating negative links [52, 53] as well as beneficial ones [6]. Lande [33] is the first one to have popularized the idea of sexual selection promoting speciation. Then numerous authors deal with it in depth [44, 45]. Furthermore, biological examples of speciation that involve well studied mechanisms of sexual selection are numerous and well documented, as the case of Hawaii cricket *Laupala* [42, 54, 38], Amazonian frog *Physalaemus* [7], or the cichlid fish species of Lake Victoria [49]. Modelling approaches allow to investigate the relative roles of stochastic processes, ecological factors, and sexual selection in limiting gene flow. The role of so-called 'magic' or 'multiple effect' traits, which associate both adaptation to a new ecological niche and a mate preference as enhancer of speciation as been evidenced in many experimental studies [39] as well as theoretical ones [34, 56]. However, identifying the role of sexual selection itself as trigger of speciation without ecological adaptation has received less attention [21], although some authors have illustrated the promoting role of sexual preference alone, using numerical simulations [31, 40]. In this paper, we aim at introducing and studying mathematically a stochastic model accounting for the stopping of gene flow between two subpopulations by means of sexual preference only.

We consider a population of haploid individuals characterized by their genotype at one multi-allelic locus, and by their position on a space that is divided in several patches. This population is modeled by a multi-type birth and death process with competition, which is ecologically neutral in the sense that individuals with different genotypes are not characterized by different adaptations to environment or by different resource preferences. However,

individuals reproduce sexually according to mating preferences that depend on their genotype: two individuals having the same genotype have a higher probability of mating success. This assortative mating situation (assortative mating by phenotype matching) has been highlighted notably in plant species, in particular due to simultaneous maturation of male and female reproductive organs [25, 47], and its selective advantages have been studied and modeled by Darwin [16] and more recently in the review [29]. This review provides a detailed description of these models, as well as some empirical examples supporting mate preference evolution. In addition to this sexual preference, individuals can migrate from one patch to another, at a rate depending on the frequency of individuals carrying the other genotype and living in the same patch. Examples of animals migrating to find suitable mates are well documented [48, 27]. A migration mechanism similar to the one presented in our paper has been studied in [43] in a continuous space model.

The class of stochastic individual-based models with competition and varying population size we are studying have been introduced in [5, 17] and made rigorous in a probabilistic setting in the seminal paper of Fournier and Méléard [19]. Then they have been studied notably in [9, 10, 15, 36]. Initially restricted to asexual populations, such models have evolved to incorporate the case of sexual reproduction, in both haploid [55] and diploid [13, 14, 8] populations. In [46] the authors considered both random and assortative mating in a phenotypically structured population. Our approach differs in three main points: first we consider assortative mating for ecologically equivalent populations, to study the role of sexual preference by itself. Second, the mechanism of sexual preference is different. In our model, individuals encounter uniformly with each other but have a higher probability of mating success if they are similar. Rudnicki and Zwoleński on the contrary consider that similar individuals have a higher probability to encounter and mate, but that all couples of mating individuals generate an offspring with the same probability. Finally, they do not consider any migration in their model.

We study both the stochastic individual-based model and its deterministic limit in large population. We give a complete description of the equilibria of the limiting deterministic dynamical system, and prove that the stable equilibria are the ones where only one genotype survives in each patch. We use classical arguments based on Lyapunov functions [35, 11] to derive the convergence at exponential speed of the solution to one of the stable equilibria, depending on the initial condition. Our theoretical results hold for small migration rates but we conjecture using simulations that they hold for all the possible migration rates. This fine study of the large population limit is essential to derive the behaviour of the stochastic process. Using coupling techniques with branching processes, we derive bounds for the time needed for speciation to occur in the stochastic process. These bounds are explicit functions of the individual birth rate and the mating preference parameter. Besides, we propose several generalisations of our model, and prove that our findings are robust for those generalisations.

The structure of the paper is the following. In Section 1 we describe the model and present the main results. Section 2 is devoted to a discussion on the biological assumptions of the model. In Sections 3 and 4 we state properties of the deterministic limit and of the stochastic population process, respectively. They are key tools in the proofs of the main results, which are then completed. In Section 5 we illustrate our findings and make conjecture on a more general result with the help of numerical simulations. Section 6 is devoted to some generalisations of the model. Finally, we state in the Appendix technical results needed in the proofs.

## 1. MODEL AND MAIN RESULTS

We consider a sexual haploid population with Mendelian reproduction ([23], chap. 3). Each individual carries an allele belonging to the genetic type space  $\mathcal{A} := \{A, a\}$ , and lives

in a patch  $i$  in  $\mathcal{I} = \{1, 2\}$ . We denote by  $\mathcal{E} = \mathcal{A} \times \mathcal{I}$  the type space, by  $(\mathbf{e}_{\alpha,i}, (\alpha, i) \in \mathcal{E})$  the canonical basis of  $\mathbb{R}^{\mathcal{E}}$ , and by  $\bar{\alpha}$  the complement of  $\alpha$  in  $\mathcal{A}$ . The population is modeled by a multi-type birth and death process with values in  $\mathbb{N}^{\mathcal{E}}$ . More precisely, if we denote by  $n_{\alpha,i}$  the current number of  $\alpha$ -individuals in the patch  $i$  and by  $\mathbf{n} = (n_{\alpha,i}, (\alpha, i) \in \mathcal{E})$  the current state of the population, then the birth rate of an  $\alpha$ -individual in the patch  $i$  writes

$$(1.1) \quad \lambda_{\alpha,i}(\mathbf{n}) = b \left( n_{\alpha,i} \beta \frac{n_{\alpha,i}}{n_{\alpha,i} + n_{\bar{\alpha},i}} + \frac{1}{2} n_{\alpha,i} \frac{n_{\bar{\alpha},i}}{n_{\alpha,i} + n_{\bar{\alpha},i}} + \frac{1}{2} n_{\bar{\alpha},i} \frac{n_{\alpha,i}}{n_{\alpha,i} + n_{\bar{\alpha},i}} \right) = b n_{\alpha,i} \frac{\beta n_{\alpha,i} + n_{\bar{\alpha},i}}{n_{\alpha,i} + n_{\bar{\alpha},i}}.$$

The parameter  $\beta b > 0$  scales the individual birth rate while the parameter  $\beta > 1$  represents the "mating preference" and can be interpreted as follows: two mating individuals have a probability  $\beta$  times larger to give birth to a viable offspring if they carry the same allele  $\alpha$ . This modeling of mating preferences (that are directly determined by the genome of each individual) is biologically relevant, considering [26] or [24] for instance. In the same way, the death rate of  $\alpha$ -individuals in the patch  $i$  writes

$$(1.2) \quad d_{\alpha,i}^K(\mathbf{n}) = \left( d + \frac{c}{K} (n_{\alpha,i} + n_{\bar{\alpha},i}) \right) n_{\alpha,i},$$

where  $K$  is an integer accounting for the quantity of available resources or space. This parameter is related to the concept of carrying capacity, which is the maximum population size that the environment can sustain indefinitely, and is consequently a scaling parameter for the size of the community. The individual intrinsic death rate  $d$  is assumed to be non negative and less than  $b$ :

$$(1.3) \quad 0 \leq d < b.$$

The death rate definition (1.2) implies that all the individuals are ecologically equivalent: the competition pressure does not depend on the alleles  $\alpha$  and  $\alpha'$  carried by the two individuals involved in an event of competition for food or space. The competition intensity is denoted by  $c > 0$ . Last, the migration of  $\alpha$ -individuals from patch  $\bar{i} = \mathcal{I} \setminus \{i\}$  to patch  $i$  occurs at a rate

$$(1.4) \quad \rho_{\alpha,\bar{i} \rightarrow i}(\mathbf{n}) = p \left( 1 - \frac{n_{\alpha,\bar{i}}}{n_{\alpha,\bar{i}} + n_{\bar{\alpha},\bar{i}}} \right) n_{\alpha,\bar{i}} = p \frac{n_{\alpha,\bar{i}} n_{\bar{\alpha},\bar{i}}}{n_{\alpha,\bar{i}} + n_{\bar{\alpha},\bar{i}}},$$

(see Figure 1). The individual migration rate of  $\alpha$ -individuals is proportional to the frequency of  $\bar{\alpha}$ -individuals in the patch. It reflects the fact that individuals prefer being in an environment with a majority of individuals of their own type. In particular, if all the individuals living in a patch are of the same type, there is no more migration outside this patch. Remark that the migration rate from patch  $\bar{i}$  to  $i$  is equal for  $\alpha$ - and  $\bar{\alpha}$ -individuals, hence to simplify notation, we denote

$$\rho_{\bar{i} \rightarrow i}(\mathbf{n}) = \rho_{\alpha,\bar{i} \rightarrow i}(\mathbf{n}) = \rho_{\bar{\alpha},\bar{i} \rightarrow i}(\mathbf{n}).$$

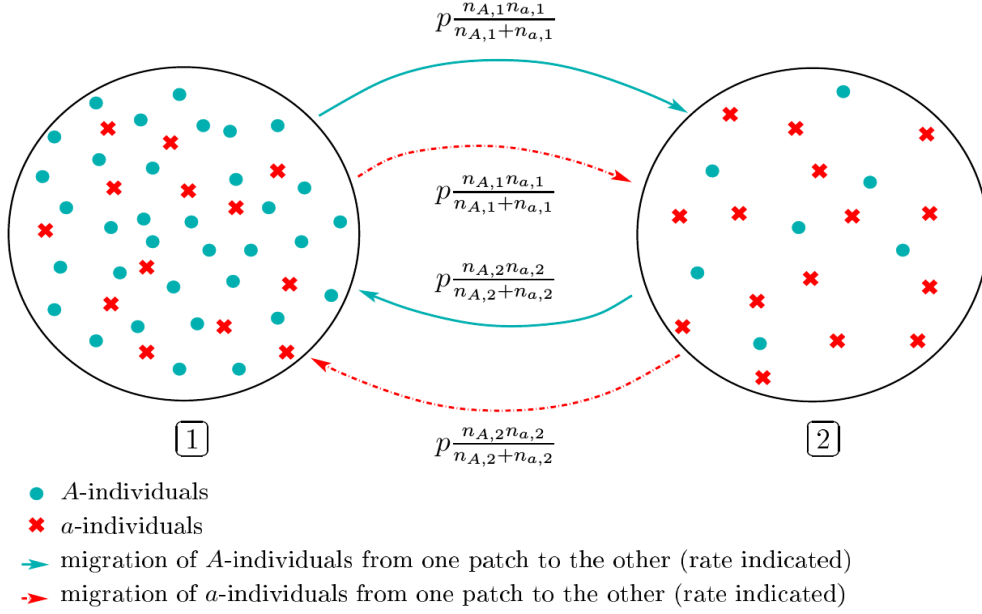
A biological discussion of the model is provided in Section 2. Besides, extensions of this model are presented and studied in Section 6.

The community is therefore represented at all time  $t \geq 0$  by a stochastic process with values in  $\mathbb{R}^{\mathcal{E}}$ :

$$(\mathbf{N}^K(t), t \geq 0) = (N_{\alpha,i}^K(t), (\alpha, i) \in \mathcal{E}, t \geq 0),$$

whose transitions are, for  $\mathbf{n} \in \mathbb{N}^{\mathcal{E}}$  and  $(\alpha, i) \in \mathcal{E}$ :

$$\begin{aligned} \mathbf{n} &\longrightarrow \mathbf{n} + \mathbf{e}_{\alpha,i} && \text{at rate } \lambda_{\alpha,i}(\mathbf{n}), \\ &\longrightarrow \mathbf{n} - \mathbf{e}_{\alpha,i} && \text{at rate } d_{\alpha,i}^K(\mathbf{n}), \\ &\longrightarrow \mathbf{n} + \mathbf{e}_{\alpha,i} - \mathbf{e}_{\alpha,\bar{i}} && \text{at rate } \rho_{\bar{i} \rightarrow i}(\mathbf{n}). \end{aligned}$$

FIGURE 1. Migrations of  $A$ - and  $a$ -individuals between the patches.

As originally done by Fournier and Méléard [19], it is convenient to represent a trajectory of the process  $\mathbf{N}^K$  as the unique solution of a system of stochastic differential equations driven by Poisson point measures. We introduce twelve independent Poisson point measures  $(R_{\alpha,i}, M_{\alpha,i}, D_{\alpha,i}, (\alpha, i) \in \mathcal{E})$  on  $\mathbb{R}_+^2$  with intensity  $ds d\theta$ . These measures represent respectively the birth, migration and death events in the population  $N_{\alpha,i}^K$ . We obtain for every  $t \geq 0$ ,

$$\begin{aligned}
 \mathbf{N}^K(t) = \mathbf{N}^K(0) + \sum_{(\alpha,i) \in \mathcal{E}} \bigg[ & \int_0^t \int_0^\infty \mathbf{e}_{\alpha,i} \mathbf{1}_{\{\theta \leq \lambda_{\alpha,i}(\mathbf{N}^K(s-))\}} R_{\alpha,i}(ds, d\theta) \\
 & - \int_0^t \int_0^\infty \mathbf{e}_{\alpha,i} \mathbf{1}_{\{\theta \leq d_{\alpha,i}^K(\mathbf{N}^K(s-))\}} D_{\alpha,i}(ds, d\theta) \\
 & + \int_0^t \int_0^\infty (\mathbf{e}_{\alpha,\bar{i}} - \mathbf{e}_{\alpha,i}) \mathbf{1}_{\{\theta \leq \rho_{\bar{i} \rightarrow i}(\mathbf{N}^K(s-))\}} M_{\alpha,i}(ds, d\theta) \bigg].
 \end{aligned}
 \tag{1.5}$$

In the sequel, we will assume that the initial population sizes  $(N_{\alpha,i}^K(0), (\alpha, i) \in \mathcal{E})$  are of order  $K$ . As a consequence, we consider a rescaled stochastic process

$$(\mathbf{Z}^K(t), t \geq 0) = (Z_{\alpha,i}^K(t), (\alpha, i) \in \mathcal{E}, t \geq 0) = \left( \frac{\mathbf{N}^K(t)}{K}, t \geq 0 \right),$$

which will be comparable to a solution of the dynamical system

$$\begin{cases}
 \frac{d}{dt} z_{A,1}(t) = z_{A,1} \left[ b \frac{\beta z_{A,1} + z_{a,1}}{z_{A,1} + z_{a,1}} - d - c(z_{A,1} + z_{a,1}) - p \frac{z_{a,1}}{z_{A,1} + z_{a,1}} \right] + p \frac{z_{A,2} z_{a,2}}{z_{A,2} + z_{a,2}} \\
 \frac{d}{dt} z_{a,1}(t) = z_{a,1} \left[ b \frac{\beta z_{a,1} + z_{A,1}}{z_{A,1} + z_{a,1}} - d - c(z_{A,1} + z_{a,1}) - p \frac{z_{A,1}}{z_{A,1} + z_{a,1}} \right] + p \frac{z_{A,2} z_{a,2}}{z_{A,2} + z_{a,2}} \\
 \frac{d}{dt} z_{A,2}(t) = z_{A,2} \left[ b \frac{\beta z_{A,2} + z_{a,2}}{z_{A,2} + z_{a,2}} - d - c(z_{A,2} + z_{a,2}) - p \frac{z_{a,2}}{z_{A,2} + z_{a,2}} \right] + p \frac{z_{A,1} z_{a,1}}{z_{A,1} + z_{a,1}} \\
 \frac{d}{dt} z_{a,2}(t) = z_{a,2} \left[ b \frac{\beta z_{a,2} + z_{A,2}}{z_{A,2} + z_{a,2}} - d - c(z_{A,2} + z_{a,2}) - p \frac{z_{A,2}}{z_{A,2} + z_{a,2}} \right] + p \frac{z_{A,1} z_{a,1}}{z_{A,1} + z_{a,1}}.
 \end{cases}
 \tag{1.6}$$

More precisely, let us denote by

$$(\mathbf{z}^{(z^0)}(t), t \geq 0) = (z_{\alpha,i}^{(z^0)}(t), (\alpha, i) \in \mathcal{E})_{t \geq 0}$$

the unique solution to (1.6) starting from  $\mathbf{z}(0) = \mathbf{z}^0 \in \mathbb{R}_+^{\mathcal{E}}$ . The uniqueness derives from the fact that the vector field is locally lipschitz and that the solutions do not explode in finite time [11]. We have the following classical approximation result which will be proven in Appendix A:

**Lemma 1.1.** *Let  $T$  be in  $\mathbb{R}_+^*$ . Assume that the sequence  $(\mathbf{Z}^K(0), K \geq 1)$  converges in probability when  $K$  goes to infinity to a deterministic vector  $\mathbf{z}^0 \in \mathbb{R}_+^{\mathcal{E}}$ . Then*

$$(1.7) \quad \lim_{K \rightarrow \infty} \sup_{s \leq T} \|\mathbf{Z}^K(s) - \mathbf{z}^{(\mathbf{z}^0)}(s)\| = 0 \quad \text{in probability,}$$

where  $\|\cdot\|$  denotes the  $L^\infty$ -Norm on  $\mathbb{R}^{\mathcal{E}}$ .

When  $K$  is large, this convergence result allows one to derive the global behaviour of the population process  $\mathbf{N}^K$  from the behaviour of the differential system (1.6). Therefore, a fine study of (1.6) is needed. To this aim, let us introduce the parameter

$$(1.8) \quad \zeta := \frac{\beta b - d}{c},$$

which corresponds to the equilibrium of the  $\alpha$ -population size for the dynamical system (1.6), in a patch with no  $\bar{\alpha}$ -individuals and no migration. Let us also define the parameters

$$(1.9) \quad \tilde{\zeta} := \frac{b^2(\beta^2 - 1) + 2p(b - d) - 2bd(\beta - 1)}{4c(b(\beta - 1) + p)} \quad \text{and} \quad \Delta := \zeta \left( \zeta - 2p \frac{\tilde{\zeta}}{b(\beta - 1) + p} \right) > 0$$

(see (3.7) for the positivity of  $\Delta$ ). We derive in Section 3 the following properties of the dynamical system (1.6):

**Theorem 1.** (1) *For  $\beta \geq 1$ , the following points for which only one type remains, in only one patch*

$$(1.10) \quad (\zeta, 0, 0, 0) \quad (0, \zeta, 0, 0) \quad (0, 0, \zeta, 0) \quad (0, 0, 0, \zeta)$$

*are non-null and non-negative equilibria of the dynamical system (1.6).*

(2) *For  $\beta > 1$ , the remaining non-null and non-negative fixed points are exactly:*

- *Equilibria for which each type is present in exactly one patch*

$$(1.11) \quad (\zeta, 0, 0, \zeta), \quad (0, \zeta, \zeta, 0)$$

- *Equilibria for which only one type remains present, in both patches*

$$(1.12) \quad (\zeta, 0, \zeta, 0), \quad (0, \zeta, 0, \zeta)$$

- *Equilibria with both types remaining in both patches*

$$(1.13) \quad \left( \frac{b(\beta + 1) - 2d}{4c}, \frac{b(\beta + 1) - 2d}{4c}, \frac{b(\beta + 1) - 2d}{4c}, \frac{b(\beta + 1) - 2d}{4c} \right)$$

$$(1.14) \quad \left( \frac{\zeta + \sqrt{\Delta}}{2}, \frac{\zeta - \sqrt{\Delta}}{2}, \tilde{\zeta}, \tilde{\zeta} \right), \quad \left( \frac{\zeta - \sqrt{\Delta}}{2}, \frac{\zeta + \sqrt{\Delta}}{2}, \tilde{\zeta}, \tilde{\zeta} \right),$$

$$(1.15) \quad \left( \tilde{\zeta}, \tilde{\zeta}, \frac{\zeta + \sqrt{\Delta}}{2}, \frac{\zeta - \sqrt{\Delta}}{2} \right), \quad \left( \tilde{\zeta}, \tilde{\zeta}, \frac{\zeta - \sqrt{\Delta}}{2}, \frac{\zeta + \sqrt{\Delta}}{2} \right).$$

*The only stable equilibria of the dynamical system (1.6) are those defined in Equation (1.11), for which each of the two alleles is present in exactly one patch, and those given in Equation (1.12) for which only one type remains.*

- (3) For  $\beta = 1$ , the remaining non-null and non-negative fixed points are exactly the two sets

$$\mathcal{L} = \{\mathbf{u}(x) = (\zeta - x, x, x, \zeta - x), x \in [0, \zeta]\}$$

and

$$\tilde{\mathcal{L}} = \{\tilde{\mathbf{u}}(x) = (\zeta - x, x, \zeta - x, x), x \in [0, \zeta]\}.$$

Those equilibria are non-hyperbolic. For any  $x \in [0, \zeta] \setminus \{\zeta/2\}$ , the Jacobian matrix at the equilibrium  $\mathbf{u}(x)$  admits 0 as an eigenvalue (associated with the eigenvector  $(1, -1, -1, 1)$ , direction of the line  $\mathcal{L}$ ) and three negative eigenvalues. Some symmetrical results hold for  $\tilde{\mathbf{u}}(x)$ . The Jacobian matrix at the equilibrium  $\mathbf{u}(\zeta/2) = \tilde{\mathbf{u}}(\zeta/2)$  admits two negative eigenvalues and the eigenvalue 0 which is of multiplicity two.

The equilibria (1.11) and (1.12) correspond to the case where reproductive isolation occurs since the gene flow between the two patches ends to be null. The dynamics of the solutions are essentially different in the cases  $\beta > 1$  and  $\beta = 1$ . They converge to an equilibrium without gene flow when  $\beta > 1$ , whereas when  $\beta = 1$ , depending on the initial condition, the solutions will converge to different equilibria with a nonzero migration rate, that is without reproductive isolation. The following proposition states that for each  $x$ , we can construct particular trajectories of the system which converge to  $\mathbf{u}(x)$ .

**Proposition 1.1.** *Let us introduce for any  $w \in (0, +\infty)$  and  $x \in [0, w]$  the vector*

$$\mathbf{v}(w, x) = (w - x, x, x, w - x).$$

*The solution  $z^{(\mathbf{v}(w, x))}$  of the system (1.6) with  $\beta = 1$  such that  $z^{(\mathbf{v}(w, x))}(0) = \mathbf{v}(w, x)$  converges when  $t \rightarrow \infty$  to the equilibrium  $\mathbf{u}(\zeta x/w)$ .*

In particular, the equilibria (1.11) are not asymptotically stable when  $\beta = 1$  since solutions starting in any neighbourhood of (1.11) can converge to different equilibria. Note that the shape of the migration is not sufficient to entail reproductive isolation although it seems to reinforce the homogamy described by the  $\beta$  parameter. Thanks to simulations in Section 5, we will see that the effect of migration on the system dynamics is rather involved.

As a consequence, we assume  $\beta > 1$  in the sequel. The following theorem gives the long-time convergence of the dynamical system (1.6) toward a stable equilibrium of interest, when starting from an explicit subset of  $\mathbb{R}_+^{\mathcal{E}}$ . To state this latter, we need to define the subset of  $\mathbb{R}_+^{\mathcal{E}}$

$$(1.16) \quad \mathcal{D} := \{\mathbf{z} \in \mathbb{R}_+^{\mathcal{E}}, z_{A,1} - z_{a,1} > 0, z_{a,2} - z_{A,2} > 0\},$$

and the positive real number

$$(1.17) \quad p_0 = \frac{\sqrt{b(\beta - 1)[b(3\beta + 1) - 4d]} - b(\beta - 1)}{2}.$$

Notice that under Assumption (1.3) and as  $\beta > 1$ ,

$$p_0 < b(\beta + 1) - 2d.$$

Finally, for  $p < b(\beta + 1) - 2d$ , we introduce the set

$$(1.18) \quad \mathcal{K}_p := \left\{ \mathbf{z} \in \mathcal{D}, \{z_{A,1} + z_{a,1}, z_{A,2} + z_{a,2}\} \in \left[ \frac{b(\beta + 1) - 2d - p}{2c}, \frac{2b\beta - 2d + p}{2c} \right] \right\}.$$

Then we have the following result:

**Theorem 2.** *Let  $p < p_0$ . Then*

- *Any solution to (1.6) which starts from  $\mathcal{D}$  converges to the equilibrium  $(\zeta, 0, 0, \zeta)$ .*

- If the initial condition of (1.6) lies in  $\mathcal{K}_p$ , there exist two positive constants  $k_1$  and  $k_2$ , depending on the initial condition, such that for every  $t \geq 0$ ,

$$\|\mathbf{z}(t) - (\zeta, 0, 0, \zeta)\| \leq k_1 e^{-k_2 t}.$$

Symmetrical results hold for the equilibria  $(0, \zeta, \zeta, 0)$ ,  $(\zeta, 0, \zeta, 0)$  and  $(0, \zeta, 0, \zeta)$ .

Note that the limit reached depends on the genotype which is initially in majority in each patch, since the subset  $\mathcal{D}$  is invariant under the dynamical system (1.6). Secondly, when  $p = 0$ , the results of Theorem 2 can be proven easily since the two patches are independent from each other. The difficulty is thus to prove the result when  $p > 0$ . Our argument allows us to deduce an explicit constant  $p_0$  under which we have convergence to an equilibrium with reproductive isolation between patches. However, we are not able to deduce a rigorous result for all  $p$ . Indeed, when  $p$  increases, there are more mixing between the two patches which makes the model difficult to study. Nevertheless simulations in Section 5 suggest that the result stays true.

Let us now introduce our main result on the probability and the time needed for the stochastic process  $\mathbf{N}^K$  to reach a neighbourhood of the equilibria defined in (1.11).

**Theorem 3.** Assume that  $\mathbf{Z}^K(0)$  converges in probability to a deterministic vector  $\mathbf{z}^0$  belonging to  $\mathcal{D}$ , with  $(z_{a,1}^0, z_{A,2}^0) \neq (0, 0)$ . Introduce the following bounded set depending on  $\varepsilon > 0$ :

$$\mathcal{B}_\varepsilon := [(\zeta - \varepsilon)K, (\zeta + \varepsilon)K] \times \{0\} \times \{0\} \times [(\zeta - \varepsilon)K, (\zeta + \varepsilon)K].$$

Then there exist three positive constants  $\varepsilon_0$ ,  $C_0$  and  $m$ , and a positive constant  $V$  depending on  $(m, \varepsilon_0)$  such that if  $p < p_0$  and  $\varepsilon \leq \varepsilon_0$ ,

$$(1.19) \quad \lim_{K \rightarrow \infty} \mathbb{P} \left( \left| \frac{T_{\mathcal{B}_\varepsilon}^K}{\log K} - \frac{1}{b(\beta - 1)} \right| \leq C_0 \varepsilon, \mathbf{N}^K(T_{\mathcal{B}_\varepsilon}^K + t) \in \mathcal{B}_{m\varepsilon} \forall t \leq e^{VK} \right) = 1,$$

where  $T_{\mathcal{B}}^K$ ,  $\mathcal{B} \subset \mathbb{R}_+^\mathcal{E}$  is the hitting time of the set  $\mathcal{B}$  by the population process  $\mathbf{N}^K$ .

Symmetrical results hold for the equilibria  $(0, \zeta, \zeta, 0)$ ,  $(\zeta, 0, \zeta, 0)$  and  $(0, \zeta, 0, \zeta)$ .

The assumption  $(z_{a,1}^0, z_{A,2}^0) \neq (0, 0)$  is necessary to get the lower bound in (1.19). Indeed, if  $(z_{a,1}^0, z_{A,2}^0) = (0, 0)$ , the set  $\mathcal{B}_\varepsilon$  is reached faster, and thus only the upper bound still holds. In this case, the speed to reach the set  $\mathcal{B}_\varepsilon$  will depend on the speed of convergence of the sequence  $(Z_{a,1}^K, Z_{A,2}^K)$  to the limit  $(0, 0)$ . In the trivial example where  $(Z_{a,1}^K, Z_{A,2}^K) = (0, 0)$ ,  $T_{\mathcal{B}}^K$  will be of order 1 which is the time needed for the processes  $Z_{A,1}^K$  and  $Z_{a,2}^K$  to reach a neighbourhood of the equilibrium  $\zeta$ . Secondly, observe that the time needed to reach a reproductive isolation is inversely proportional to  $\beta - 1$  which, as studied previously, suggests that the system behaves differently for  $\beta = 1$ . Moreover, note that it does not depend on the parameter  $p$ . Indeed, the time needed to reach a neighbourhood of the state  $(\zeta, 0, 0, \zeta)$  is of order 1, and from this neighbourhood the time needed for the complete extinction of the  $a$ -individuals in the patch 1 and the  $A$ -individuals in the patch 2 is much longer: it is of order  $\log K$ . During this second phase, the migrations between the two patches are already balanced, hence the parameter  $p$  does not appear in the constant before  $\log K$ . Furthermore, the constant does not depend on  $d$  and  $c$  since there is no ecological difference between the two types and the two patches. Indeed, during the second phase, the natural birth rate of the  $a$ -individuals in the patch 1 is approximately  $b$  since the patch 1 is almost entirely filled with  $A$ -individuals, and their natural death rate can be approximated by  $d + c\zeta = b\beta$  where the term  $c\zeta$  comes from the competition exerted by the  $A$ -individuals. Thus, their natural growth rate is approximately  $b - b\beta$  which only depends on the birth parameters. Finally, Theorem 3 gives not only an estimation of the time to reach a neighbourhood of the

limit, but also it proves that the dynamics of the population process stays a long time in the neighbourhood of equilibria (1.11) after this time.

## 2. DISCUSSION OF THE MODEL

**Assortative mating.** Assortative mating can result from different factors. In our model (as in [32] for instance), the birth rate of an individual with genotype  $\alpha$  in the deme  $i$  is equal to

$$(2.1) \quad bn_{\alpha,i} \frac{\beta n_{\alpha,i} + n_{\bar{\alpha},i}}{n_{\alpha,i} + n_{\bar{\alpha},i}}.$$

This equation models assortative mating by phenotypic matching. This can be due to an increased genetic compatibility or to an increased mating probability after encountering of individuals with the same phenotype, assuming that all individuals encounter each other uniformly at random.

In [51] or [30], the birth rate of an individual with genotype  $\alpha$  in the deme  $i$  is equal to

$$(2.2) \quad bn_{\alpha,i} \frac{\beta n_{\alpha,i} + \frac{1}{2}n_{\bar{\alpha},i}}{\beta n_{\alpha,i} + n_{\bar{\alpha},i}} + bn_{\bar{\alpha},i} \frac{\frac{1}{2}n_{\alpha,i}}{n_{\alpha,i} + \beta n_{\bar{\alpha},i}}.$$

In this case, the authors model assortative mating due to non-uniform meeting of mates, depending on their respective genotypes.

The shapes of the birth rates in (2.1) and (2.2) can be seen as limiting cases of a general model introduced in [22]. In this model, individuals are diploid, with genotypes  $AA$ ,  $Aa$  or  $aa$ , males and females are distinguished, and generations do not overlap. Males and females encounter randomly and females mate only once in each generation. If a female does not mate with a given male, she can mate with the next male she encounters, and so on. If she does not mate after the  $n$ th encounter, she does not produce any offspring in the next generation. The parameter  $n$  depends on the time duration of the reproduction period. When  $n = 1$  the overall frequency of  $AA \times AA$  matings in the population is  $\alpha x_{AA}^2$ , where  $\alpha$  is a preference parameter and  $x_{AA}$  is the frequency of individuals of type  $AA$ . This expression is similar to the one of our model. When  $n$  goes to infinity, this frequency becomes  $\alpha x_{AA}^2 / (\alpha x_{AA} + \beta x_{Aa} + \gamma x_{aa})$ , with the same interpretation for the parameters, leading to an expression similar to the one in [51, 30].

As an example, our definition of assortative mating can model reproduction of hermaphroditic plants with uniform pollen dispersal within each deme and simultaneous maturation of both male and female reproductive organs, at a time that depends on the plant genotype, as studied in [25, 47]. Alternatively, we can think of high density populations of milkweed longhorn beetle *Tetraopes tetraophthalmus* where assortative mating is strong because at high density, large males are more likely to interfere with small males' copulation with large females [37]. In this case, assortative mating is not adaptive but rather depends on the life conditions of the population. We can find other examples of this type in a recent review on assortative mating in animals [28].

**Cost of choosiness.** In this article, we do not really integrate any cost of choosiness. More precisely, we assume a constant availability of both male and female organs of hermaphroditic individuals (like in sponges, sea anemones, tapeworms, snails, earthworms, or some fishes [3] for instance). Cost of choosiness for populations having specific mating periods and limited mating trials have been studied in [32]. Integrating cost of choosiness is useful when studying the apparition and the evolution of mating preferences, as done in [32] or [4].



**Initial conditions.** Concerning the initial allelic diversity, which is a question highly debated in the literature on speciation [57], we have in mind populations where traits evolved neutrally before taking part in mating preferences after a change in the environment or a migration of the population to a new environment. For example, it is the case for the two sister species *P. nyererei* and *P. pundamilia*. Males of these two species have different nuptial colorations (red and blue, respectively), and females of these two species have preferences for a specific male nuptial coloration in clear water (red for *P. nyererei* and blue for *P. pundamilia*). These mating preferences have been proven to be inheritable [24], and uniformly random mating in turbid water has been inferred from phenotype frequency distribution in nature [50].

**Migration.** In our model the migration rate of a given individual is proportional to the proportion of individuals that do not have the same genotype as the considered individual. The idea is that an individual is more prone to move if it does not find suitable mates in its deme. This particular form of mating success dependent dispersal has also been studied in [43] for a continuous space. Correlations between male dispersal and mating success have been empirically observed in [48] or [27] for instance.

### 3. STUDY OF THE DYNAMICAL SYSTEM

In this section, we study the dynamical system (1.6) in order to prove Theorems 1 and 2. In the first subsection, we are concerned with the equilibria of (1.6) and their local stability (Theorem 1). In the second subsection, we look more closely at the case where the migration rate  $p$  is lower than  $p_0$  and prove the convergence of the solution to (1.6) towards one of the equilibria with an exponential rate once the trajectory belongs to  $\mathcal{K}_p$  (Theorem 2).

**3.1. Fixed points and stability when  $\beta > 1$ .** First of all, we prove that all nonnegative and non-zero stationary points of (1.6) are given in Theorem 1. Let us write the four equations defining equilibria  $(z_{A,1}, z_{a,1}, z_{A,2}, z_{a,2})$  of the dynamical system (1.6):

$$(3.1) \quad z_{A,1} \left[ b \frac{\beta z_{A,1} + z_{a,1}}{z_{A,1} + z_{a,1}} - d - c(z_{A,1} + z_{a,1}) - p \frac{z_{a,1}}{z_{A,1} + z_{a,1}} \right] + p \frac{z_{A,2} z_{a,2}}{z_{A,2} + z_{a,2}} = 0,$$

$$(3.2) \quad z_{a,1} \left[ b \frac{\beta z_{a,1} + z_{A,1}}{z_{A,1} + z_{a,1}} - d - c(z_{A,1} + z_{a,1}) - p \frac{z_{A,1}}{z_{A,1} + z_{a,1}} \right] + p \frac{z_{A,2} z_{a,2}}{z_{A,2} + z_{a,2}} = 0,$$

$$(3.3) \quad z_{A,2} \left[ b \frac{\beta z_{A,2} + z_{a,2}}{z_{A,2} + z_{a,2}} - d - c(z_{A,2} + z_{a,2}) - p \frac{z_{a,2}}{z_{A,2} + z_{a,2}} \right] + p \frac{z_{A,1} z_{a,1}}{z_{A,1} + z_{a,1}} = 0,$$

$$(3.4) \quad z_{a,2} \left[ b \frac{\beta z_{a,2} + z_{A,2}}{z_{A,2} + z_{a,2}} - d - c(z_{A,2} + z_{a,2}) - p \frac{z_{A,2}}{z_{A,2} + z_{a,2}} \right] + p \frac{z_{A,1} z_{a,1}}{z_{A,1} + z_{a,1}} = 0.$$

By subtracting (3.1) and (3.2), and (3.3) and (3.4) we get

$$(z_{A,i} - z_{a,i}) \left( b\beta - d - c(z_{A,i} + z_{a,i}) \right) = 0, \quad i \in \mathcal{I}.$$

Therefore equilibria are defined by the four following cases:

$$\begin{cases} z_{A,1} = z_{a,1} \\ \text{or} \\ z_{A,1} + z_{a,1} = (b\beta - d)/c \end{cases} \quad \text{and} \quad \begin{cases} z_{A,2} = z_{a,2} \\ \text{or} \\ z_{A,2} + z_{a,2} = (b\beta - d)/c. \end{cases}$$

**1st case:**  $z_{A,1} = z_{a,1}$  and  $z_{A,2} = z_{a,2}$ .

From (3.1) and (3.3) we derive

$$z_{A,1} \left[ b \frac{(\beta + 1)}{2} - d - 2cz_{A,1} - \frac{p}{2} \right] = -\frac{z_{A,2}p}{2},$$

and

$$-\frac{z_{A,1}p}{2} = z_{A,2} \left[ b \frac{(\beta+1)}{2} - d - 2cz_{A,2} - \frac{p}{2} \right].$$

By summing, we get  $P(z_{A,1}) = P(z_{A,2})$  where  $P$  is the polynomial function defined by:

$$P(X) = X \left[ b \frac{(\beta+1)}{2} - d - p \right] - 2cX^2,$$

whose roots are 0 and

$$\frac{b(\beta+1) - 2d - 2p}{4c}.$$

Then, either  $z_{A,1} = z_{A,2}$  or  $z_{A,1}$  and  $z_{A,2}$  are symmetrical with respect to the maximum of  $P$  which leads to

$$z_{A,1} = \frac{b(\beta+1) - 2d - 2p}{4c} - z_{A,2}.$$

In the first case  $z_{A,1} = z_{A,2}$ , Equation (3.1) implies that either  $z_{A,1} = 0$ , which gives the null equilibrium or

$$z_{A,1} = \frac{b(\beta+1) - 2d}{4c},$$

which gives equilibrium (1.13). In the second case, we inject the expression of  $z_{A,2}$  in (3.1) to obtain that  $z_{A,1}$  satisfies:

$$-2cX^2 + AX + \frac{p}{4c}A = 0,$$

with  $A = b(\beta+1)/2 - d - p$ . The discriminant of this degree 2 equation is  $A(A+2p)$ . Therefore, either

$$z_{A,1} = \frac{A + \sqrt{A(A+2p)}}{4c} \quad \text{and} \quad z_{A,2} = \frac{A - \sqrt{A(A+2p)}}{4c},$$

or

$$z_{A,1} = \frac{A - \sqrt{A(A+2p)}}{4c} \quad \text{and} \quad z_{A,2} = \frac{A + \sqrt{A(A+2p)}}{4c}.$$

However, these equilibria are not positive.

**2nd case** :  $z_{A,1} + z_{a,1} = (b\beta - d)/c = \zeta = z_{A,2} + z_{a,2}$ .

As previously, we obtain

$$(b(\beta-1) + p)z_{A,1} \left( \frac{z_{A,1}}{\zeta} - 1 \right) = pz_{A,2} \left( \frac{z_{A,2}}{\zeta} - 1 \right),$$

and

$$pz_{A,1} \left( \frac{z_{A,1}}{\zeta} - 1 \right) = (b(\beta-1) + p)z_{A,2} \left( \frac{z_{A,2}}{\zeta} - 1 \right).$$

By summing these equalities, we get  $Q(z_{A,1}) = Q(z_{A,2})$  with

$$Q(X) = X \left( \frac{X}{\zeta} - 1 \right) (b(\beta-1) + 2p).$$

Then, either  $z_{A,1} = z_{A,2}$  and (3.1) gives that

$$z_{A,1} \left( \frac{z_{A,1}}{\zeta} - 1 \right) = 0,$$

which gives equilibrium (1.12), or  $z_{A,1} = \zeta - z_{A,2}$  which implies  $z_{A,1}(z_{A,1}/\zeta - 1) = 0$  and gives equilibrium (1.11).

**3rd case** :  $z_{A,1} = z_{a,1}$ , and  $z_{A,2} + z_{a,2} = (b\beta - d)/c = \zeta$ .

Substituting in Equations (3.1) and (3.4) we get that

$$z_{A,1} \left[ b \frac{\beta+1}{2} - d - 2cz_{A,1} - \frac{p}{2} \right] + p \frac{z_{A,2}(\zeta - z_{A,2})}{\zeta} = 0,$$

and

$$(\zeta - z_{A,2}) \left[ \frac{b}{\zeta} (\beta \zeta + (1 - \beta) z_2^A) - d - c \zeta - p \frac{z_{A,2}}{\zeta} \right] + p \frac{z_{A,1}}{2} = 0.$$

Therefore, since  $\zeta = (b\beta - d)/c$ , these equations become

$$(3.5) \quad z_{A,1} = \frac{2}{p} (z_{A,2} - \zeta) z_{A,2} \left[ \frac{b(1 - \beta) - p}{\zeta} \right],$$

and

$$\frac{(z_{A,2} - \zeta) z_{A,2}}{\zeta} \left\{ \frac{2}{p} [b(1 - \beta) - p] \left[ b \frac{\beta + 1}{2} - d - \frac{p}{2} - \frac{4c}{p} (z_{A,2} - \zeta) z_{A,2} \frac{b(1 - \beta) - p}{\zeta} \right] - p \right\} = 0.$$

This last equation provides the following possible cases:

- $z_{A,2} = 0$ , which implies  $z_{a,2} = \zeta$ , and from (3.5)  $z_{A,1} = z_{a,1} = 0$  (Equilibrium (1.10)),
- $z_{A,2} = \zeta$ , which implies  $z_{a,2} = 0$ , and from (3.5)  $z_{A,1} = z_{a,1} = 0$  (Equilibrium (1.10)),
- $z_{A,2}$  solution of

$$(b(1 - \beta) - p) \left[ b \frac{\beta + 1}{2} - d - \frac{p}{2} - \frac{4c}{p} (z_{A,2} - \zeta) z_{A,2} \frac{b(1 - \beta) - p}{\zeta} \right] - \frac{p^2}{2} = 0,$$

which can be summarized as

$$(3.6) \quad (z_{A,2} - \zeta) z_{A,2} + C = 0,$$

where

$$C = \frac{p\zeta}{8c(b(\beta - 1) + p)^2} [b^2(\beta^2 - 1) + 2p(b - d) - 2bd(\beta - 1)].$$

The discriminant  $\Delta$  of the degree 2 Equation (3.6) was introduced in Equation (1.9). A simple computation gives the sign of  $\Delta$ :

$$(3.7) \quad \begin{aligned} \Delta &= \zeta^2 - 4C \\ &= \zeta^2 - \frac{p\zeta}{2c(b(\beta - 1) + p)^2} [b^2(\beta^2 - 1) + 2p(b - d) - 2bd(\beta - 1)] \\ &= \frac{\zeta}{2c(b(\beta - 1) + p)^2} \left[ 2b^2(\beta - 1)^2(b\beta - d) \right. \\ &\quad \left. + 2bp(\beta - 1)[b\beta - d + p] + b^2(\beta - 1)^2p \right] > 0. \end{aligned}$$

Thus (3.6) has two distinct solutions:

$$z_{A,2}^+ = \frac{\zeta + \sqrt{\Delta}}{2} > 0 \quad \text{and} \quad z_{A,2}^- = \frac{\zeta - \sqrt{\Delta}}{2}.$$

Since  $C > 0$ , both roots  $z_{A,2}^-$  and  $z_{A,2}^+$  are strictly positive.

We finally deduce from (3.5) and (3.6) that in both cases  $z_{A,2} = z_{A,2}^-$  and  $z_{A,2} = z_{A,2}^+$  then

$$z_{A,1} = z_{a,1} = \frac{b^2(\beta^2 - 1) + 2p(b - d) - 2bd(\beta - 1)}{4c(b(\beta - 1) + p)}.$$

This gives equilibrium (1.14), by symmetry between patches 1 and 2.

The end of this subsection provides a detailed exposition of the stability of fixed points of (1.6). We consider separately each equilibrium and use symmetries of the dynamical system between patches 1 and 2 and between alleles  $A$  and  $a$ .

**Equilibrium (1.10):** By subtracting (3.2) from (3.1), we obtain:

$$(3.8) \quad \frac{d}{dt} (z_{A,1} - z_{a,1}) = (z_{A,1} - z_{a,1}) (b\beta - d - c(z_{A,1} + z_{a,1})).$$

This equation provides the asymptotic instability since for this equilibrium,  $z_{A,1} + z_{a,1} = 0$ .

**Equilibrium (1.11):** We consider the equilibrium  $(\zeta, 0, 0, \zeta)$ . The Jacobian matrix of the dynamical system at this fixed point is:

$$\begin{pmatrix} -(b\beta - d) & b(1 - 2\beta) + d - p & p & 0 \\ 0 & b(1 - \beta) - p & p & 0 \\ 0 & p & b(1 - \beta) - p & 0 \\ 0 & p & b(1 - 2\beta) + d - p & -(b\beta - d) \end{pmatrix}$$

The eigenvalues are:  $-b(\beta - 1)$ ,  $-b(\beta - 1) - 2p$ , and  $-(b\beta - d)$ . All of them are negative, and  $-(b\beta - d)$  is of multiplicity two. The equilibrium is therefore asymptotically stable.

**Equilibrium (1.12):** We consider the equilibrium  $(0, \zeta, 0, \zeta)$ . The Jacobian matrix of the dynamical system at this fixed point is:

$$\begin{pmatrix} b(1 - \beta) - p & 0 & p & 0 \\ b(1 - 2\beta) + d - p & -(b\beta - d) & p & 0 \\ p & 0 & b(1 - \beta) - p & 0 \\ p & 0 & b(1 - 2\beta) + d - p & -(b\beta - d) \end{pmatrix}$$

The eigenvalues are:  $-b(\beta - 1)$ ,  $-b(\beta - 1) - 2p$ , and  $-(b\beta - d)$ . All of them are negative, and  $-(b\beta - d)$  is of multiplicity two. The equilibrium is therefore asymptotically stable.

**Equilibrium (1.13):** The Jacobian matrix of the dynamical system at this fixed point is:

$$\frac{1}{4} \begin{pmatrix} 2(d - b) - p & 2(d - b\beta) - p & p & p \\ 2(d - b\beta) - p & 2(d - b) - p & p & p \\ p & p & 2(d - b) - p & 2(d - b\beta) - p \\ p & p & 2(d - b\beta) - p & 2(d - b) - p \end{pmatrix}$$

The eigenvalues are:  $-(b(\beta + 1)/2 - d)$ ,  $-(b(\beta + 1)/2 - d + p)$  and  $b(\beta - 1)/2$ .  $-(b(\beta + 1)/2 - d)$  and  $-(b(\beta + 1)/2 - d + p)$  are negative, and  $b(\beta - 1)/2$  is positive and of multiplicity two. The equilibrium is thus unstable.

**Equilibrium (1.14):** Recall the definition of  $\tilde{\zeta}$  in (1.9) and assume that  $z_{A,1} = z_{a,1} = \tilde{\zeta}$ . We first prove that at this fixed point,

$$(3.9) \quad z_{A,1} + z_{a,1} = 2\tilde{\zeta} < \zeta,$$

which is equivalent to

$$b^2(\beta^2 - 1) + 2p(b - d) - 2bd(\beta - 1) < 2(b(\beta - 1) + p)(b\beta - d).$$

A straightforward computation leads to

$$b^2(\beta^2 - 1) + 2p(b - d) - 2bd(\beta - 1) - 2(b(\beta - 1) + p)(b\beta - d) = -b(\beta - 1)(2p + b(\beta - 1)),$$

which is negative and thus proves the inequality. From (3.9) we deduce that near the equilibrium (1.14),  $b\beta - d - c(z_{A,1} + z_{a,1}) > 0$ . The instability then derives from Equation (3.8).

**3.2. Fixed points and stability when  $\beta = 1$ .** Following a similar reasoning to the one in Section 3.1, we obtain that the equilibria of the system are exactly the lines  $\mathcal{L}$  and  $\tilde{\mathcal{L}}$  defined in Theorem 1. A study of the Jacobian matrices proves that these equilibria are no longer hyperbolic. It ends the proof of Theorem 1.

**3.3. Proof of Proposition 1.1.** This subsection is devoted to the proof of Proposition 1.1. The idea is to find a solution of the form

$$\psi(t) = \gamma(t)\mathbf{v}(w, x) \quad \text{with} \quad \gamma(0) = 1,$$

where  $\mathbf{v}(w, x) = (w - x, x, x, w - x)$  has been introduced in Proposition 1.1. Assuming that  $\psi$  is solution to the system (1.6) with  $\beta = 1$ , we deduce that for all  $(\alpha, i) \in \mathcal{E}$ :

$$\begin{aligned} \frac{d}{dt}\psi_{\alpha,i}(t) &= \frac{d}{dt}\gamma(t)v_{\alpha,i}(w, x) \\ &= \psi_{\alpha,i}(t)(b - d - c(\psi_{\alpha,i}(t) + \psi_{\bar{\alpha},i}(t))) + p \frac{\psi_{\alpha,i}(t)\psi_{\bar{\alpha},i}(t)}{\psi_{\alpha,i}(t) + \psi_{\bar{\alpha},i}(t)} - p \frac{\psi_{\alpha,\bar{i}}(t)\psi_{\bar{\alpha},\bar{i}}(t)}{\psi_{\alpha,\bar{i}}(t) + \psi_{\bar{\alpha},\bar{i}}(t)} \\ &= \gamma(t)v_{\alpha,i}(w, x)(b - d - cw\gamma(t)). \end{aligned}$$

Thus  $\gamma(t)$  satisfies the logistic equation

$$\frac{d}{dt}\gamma(t) = \gamma(t)(b - d - cw\gamma(t)),$$

whose solution starting from 1 is given by

$$(3.10) \quad \gamma(t) = \frac{e^{t(b-d)}}{1 + \frac{cw}{b-d}(e^{t(b-d)} - 1)}.$$

In particular  $\gamma(t)$  converges to  $(b - d)/cw = \zeta/w$  as  $t \rightarrow \infty$ .

A standard computation proves that  $\psi(t) = \gamma(t)\mathbf{v}(w, x)$  with  $\gamma$  chosen according to (3.10) is the solution to (1.6) starting from  $\mathbf{v}(w, x)$  and converges to  $\zeta\mathbf{v}(w, x)/w = \mathbf{u}(\zeta x/w)$ . This ends the proof of Proposition 1.1.

**3.4. Containment and Lyapunov function for a small migration rate.** In this subsection, we are mainly interested in Equilibrium (1.11). Recall the definition of  $\mathcal{D}$  in (1.16)

$$\mathcal{D} := \{z \in \mathbb{R}_+^{\mathcal{E}}, z_{A,1} - z_{a,1} > 0, z_{a,2} - z_{A,2} > 0\}.$$

First, we prove that we can restrict our attention to the bounded set  $\mathcal{K}_p \subset \mathcal{D}$  defined in (1.18). For the sake of readability, we introduce the two real numbers

$$(3.11) \quad z_{\min} := \frac{b(\beta + 1) - 2d - p}{2c} \leq \zeta \leq \zeta + \frac{p}{2c} =: z_{\max},$$

which allows one to write the set  $\mathcal{K}_p$  defined in (1.18) as

$$\mathcal{K}_p := \{z \in \mathcal{D}, \{z_{A,1} + z_{a,1}, z_{A,2} + z_{a,2}\} \in [z_{\min}, z_{\max}]\}.$$

**Lemma 3.1.** *Assume that  $p < b(\beta + 1) - 2d$ . The set  $\mathcal{K}_p$  is invariant under the dynamical system (1.6). Moreover, any solution to (1.6) starting from the set  $\mathcal{D}$  reaches  $\mathcal{K}_p$  after a finite time.*

*Proof.* First, Equation (3.8) and the symmetrical equation for the patch 2 are sufficient to prove that the subset  $\mathcal{D}$  is invariant under the dynamical system.

Second, we prove that the trajectory reaches the bounded set  $\mathcal{K}_p$  in a finite time and third that  $\mathcal{K}_p$  is stable. The dynamics of the total population size  $n = z_{A,1} + z_{a,1} + z_{A,2} + z_{a,2}$  satisfies

$$\frac{dn}{dt} = n(\beta b - d) - 2b(\beta - 1) \left( \frac{z_{A,1}z_{a,1}}{z_{A,1} + z_{a,1}} + \frac{z_{A,2}z_{a,2}}{z_{A,2} + z_{a,2}} \right) - c((z_{A,1} + z_{a,1})^2 + (z_{A,2} + z_{a,2})^2).$$

Since  $(a + b)^2 \leq 2(a^2 + b^2)$  for every real numbers  $(a, b)$ ,

$$\frac{dn}{dt} \leq n \left( \beta b - d - \frac{c}{2}n \right).$$

Using classical results on logistic equations, we deduce that

$$(3.12) \quad \limsup_{t \rightarrow +\infty} n(t) \leq 2\zeta.$$

Let  $\varepsilon$  be positive, and suppose that for any  $t > 0$ ,  $(z_{A,1} + z_{a,1})(t) \leq \zeta - \varepsilon$ , then using (3.8) we have for  $t \geq 0$ ,

$$(3.13) \quad z_{A,1}(t) \geq (z_{A,1} - z_{a,1})(t) \geq (z_{A,1} - z_{a,1})(0)e^{c\varepsilon t} \xrightarrow[t \rightarrow +\infty]{} +\infty.$$

This contradicts (3.12). As a consequence,

$$(3.14) \quad \exists t < \infty, \quad (z_{A,1} + z_{a,1})(t) \geq \zeta - \varepsilon.$$

In particular, this result holds for  $\zeta - \varepsilon_0 = z_{\min}$  where  $\varepsilon_0 = (p + b(\beta - 1))/2c$ .

Furthermore, the dynamics of the total population size in the patch 1 satisfies the following equation:

$$(3.15) \quad \begin{aligned} \frac{d}{dt}(z_{A,1} + z_{a,1}) &= (z_{A,1} + z_{a,1})(b\beta - d - c(z_{A,1} + z_{a,1})) \\ &\quad - 2(b(\beta - 1) + p) \frac{z_{A,1}z_{a,1}}{z_{A,1} + z_{a,1}} + 2p \frac{z_{A,2}z_{a,2}}{z_{A,2} + z_{a,2}}. \end{aligned}$$

By noticing that  $z_{A,1}z_{a,1} \leq (z_{A,1} + z_{a,1})^2/4$ , we get

$$(3.16) \quad \begin{aligned} \frac{d}{dt}(z_{A,1} + z_{a,1}) &\geq (z_{A,1} + z_{a,1})(b\beta - d - c(z_{A,1} + z_{a,1})) - (b(\beta - 1) + p) \frac{z_{A,1} + z_{a,1}}{2} \\ &\geq c(z_{A,1} + z_{a,1})(z_{\min} - (z_{A,1} + z_{a,1})). \end{aligned}$$

The last term becomes positive as soon as  $z_{A,1} + z_{a,1} \leq z_{\min}$ . As a consequence, once the total population size in the patch 1 is larger than  $z_{\min}$ , it stays larger than this threshold. Using symmetrical arguments, the same conclusion holds for the patch 2. Using additionally (3.14), we find  $t_{\min} > 0$  such that  $\forall t \geq t_{\min}$ ,

$$(3.17) \quad z_{A,i}(t) + z_{a,i}(t) \geq z_{\min}, \quad \forall i \in \mathcal{I}, \text{ and } n(t) \leq 2\zeta + 1.$$

We now focus on the upper bound of the set  $\mathcal{K}_p$  by bounding from above the total population size in the patch  $i$ , for all  $t \geq t_{\min}$ ,

$$(3.18) \quad \begin{aligned} \frac{d}{dt}(z_{A,i} + z_{a,i}) &\leq (2\zeta + 1)(c\zeta - c(z_{A,i} + z_{a,i})) + \frac{p}{2}(2\zeta + 1) \\ &\leq c(2\zeta + 1)(z_{\max} - (z_{A,i} + z_{a,i})). \end{aligned}$$

This implies that, if  $\alpha > 0$  is fixed, there exists  $t_\alpha \geq t_{\min}$  such that  $z_{A,i}(t) + z_{a,i}(t) \leq z_{\max} + \alpha$  for all  $i \in \mathcal{I}$  and  $t \geq t_\alpha$ .

Finally, we use a proof by contradiction to ensure that the trajectory hits the compact  $\mathcal{K}_p$ . Let us assume that for any  $t \geq t_\alpha$ ,

$$(3.19) \quad z_{A,1}(t) + z_{a,1}(t) \geq z_{\max} - \alpha.$$

From (3.8), and choosing an  $\alpha < p/2c$ , we deduce that  $z_{A,1} - z_{a,1}$  converges to 0. In addition with (3.19), we find  $t'_\alpha \geq t_\alpha$  such that for any  $t \geq t'_\alpha$ ,

$$(3.20) \quad \frac{z_{A,1}(t)z_{a,1}(t)}{z_{A,1}(t) + z_{a,1}(t)} \geq \frac{1}{4}(z_{\max} - 2\alpha).$$

We insert (3.20) in the equation (3.15) to deduce that, for all  $t \geq t'_\alpha$ ,

$$\begin{aligned} \frac{d}{dt}(z_{A,1} + z_{a,1}) &\leq c(2\zeta + 1)(\zeta - (z_{A,1} + z_{a,1})) - \frac{b(\beta - 1) + p}{2}(z_{max} - 2\alpha) + \frac{p}{2}(2\zeta + 1). \\ &\leq c(2\zeta + 1)(z_{max} - 2\alpha - (z_{A,1} + z_{a,1})) + 2\alpha c(2\zeta + 1) - \frac{b(\beta - 1) + p}{2}(z_{max} - 2\alpha). \end{aligned}$$

The first term of the last line is negative under Assumption (3.19), thus, if  $\alpha$  is sufficiently small,

$$\begin{aligned} \frac{d}{dt}(z_{A,1} + z_{a,1}) &\leq -\frac{1}{2}[(b(\beta - 1) + p)z_{max}] + \alpha \left[ b(\beta - 1) + \frac{p}{2c}(2\zeta + 1) \right] \\ &\leq -\frac{1}{4}[(b(\beta - 1) + p)z_{max}]. \end{aligned} \quad (3.21)$$

This contradicts (3.19). Thus, the total population size of the patch 1 is lower than  $z_{max} - \alpha$  after a finite time. Moreover, (3.18) ensures that once the total population size of the patch 1 has reached the threshold  $z_{max}$ , it stays smaller than this threshold. Reasoning similarly for the patch 2, we finally find a finite time such that the trajectory hits the compact  $\mathcal{K}_p$  and remains in it afterwards. This ends the proof of Lemma 3.1.  $\square$

As  $\mathcal{D}$  is invariant under the dynamical system (1.6), we can consider the function  $V : \mathcal{D} \rightarrow \mathbb{R}$ :

$$(3.22) \quad V(\mathbf{z}) = \ln \left( \frac{z_{A,1} + z_{a,1}}{z_{A,1} - z_{a,1}} \right) + \ln \left( \frac{z_{a,2} + z_{A,2}}{z_{a,2} - z_{A,2}} \right).$$

It characterizes the dynamics of (1.6) on  $\mathcal{K}_p$ . Indeed, as proved in the next lemma,  $V$  is a Lyapunov function if  $p$  is sufficiently small. This will allow us to prove that the solutions to (1.6) converge to  $(\zeta, 0, 0, \zeta)$  exponentially fast as soon as their trajectory hits the set  $\mathcal{K}_p$ . Before stating the next lemma, we introduce the positive real number:

$$(3.23) \quad C_1 := \frac{1}{2} \left( \frac{2b(\beta - 1) + 2p}{z_{min}} - \frac{2p}{z_{max}} \right),$$

where  $z_{min}$  and  $z_{max}$  have been defined in (3.11). Then we have the following result:

**Lemma 3.2.** *Assume that  $p < p_0$  defined in (1.17). Then  $V(\mathbf{z}(t))$  is non-negative and non-increasing on  $\mathcal{K}_p$ , and satisfies*

$$(3.24) \quad \frac{d}{dt}V(\mathbf{z}(t)) \leq -C_1(z_{a,1}(t) + z_{A,2}(t)), \quad t \geq 0.$$

*Proof.* For  $i \in \mathcal{I}$  and  $\mathbf{z} \in \mathcal{K}_p$ ,  $z_{\alpha_i,i} - z_{\bar{\alpha}_i,i} \leq z_{\alpha_i,i} + z_{\bar{\alpha}_i,i}$ , where  $\alpha_1 = A, \alpha_2 = a$  and  $\bar{\alpha}_i = \mathcal{A} \setminus \alpha_i$ . Thus,  $V(\mathbf{z}) \geq 0$ . Now,

$$\begin{aligned} \frac{d}{dt}V(\mathbf{z}(t)) &= \frac{\dot{z}_{A,1}(t) + \dot{z}_{a,1}(t)}{z_{A,1}(t) + z_{a,1}(t)} - \frac{\dot{z}_{A,1}(t) - \dot{z}_{a,1}(t)}{z_{A,1}(t) - z_{a,1}(t)} + \frac{\dot{z}_{A,2}(t) + \dot{z}_{a,2}(t)}{z_{A,2}(t) + z_{a,2}(t)} - \frac{\dot{z}_{a,2}(t) - \dot{z}_{A,2}(t)}{z_{a,2}(t) - z_{A,2}(t)} \\ (3.25) \quad &= - \sum_{i=1,2} \frac{z_{A,i}z_{a,i}}{z_{A,i} + z_{a,i}} \left[ \frac{2b(\beta - 1) + 2p}{z_{A,i} + z_{a,i}} - \frac{2p}{z_{A,\bar{i}} + z_{a,\bar{i}}} \right], \end{aligned}$$

from (3.8) and (3.15). Thus,  $dV(\mathbf{z}(t))/dt$  is nonpositive if

$$(3.26) \quad \frac{b(\beta - 1)}{p} > \max \left\{ \frac{z_{A,1} + z_{a,1}}{z_{A,2} + z_{a,2}} - 1, \frac{z_{A,2} + z_{a,2}}{z_{A,1} + z_{a,1}} - 1 \right\}.$$

Since  $\mathbf{z}$  belongs to  $\mathcal{K}_p$ , the r.h.s of (3.26) can be bounded from above by

$$\frac{z_{max}}{z_{min}} - 1 = \frac{b(\beta - 1) + 2p}{b(\beta + 1) - 2d - p}.$$

Therefore, the condition (3.26) is satisfied if

$$\frac{b(\beta - 1)}{p} > \frac{b(\beta - 1) + 2p}{b(\beta + 1) - 2d - p},$$

that is, if

$$p < \frac{\sqrt{b(\beta - 1)[b(3\beta + 1) - 4d]} - b(\beta - 1)}{2} = p_0,$$

and under this condition,

$$\frac{2b(\beta - 1) + 2p}{z_{A,i} + z_{a,i}} - \frac{2p}{z_{A,\bar{i}} + z_{a,\bar{i}}} \geq 2C_1, \quad z \in \mathcal{K}_p, \quad i \in \mathcal{I}.$$

Moreover, as the set  $\mathcal{D}$  is invariant under the dynamical system (1.6),  $z_{A,1}$  stays larger than  $z_{a,1}$ , and

$$\frac{z_{A,1}}{z_{A,1} + z_{a,1}} \geq \frac{1}{2}.$$

In the same way,

$$\frac{z_{a,2}}{z_{A,2} + z_{a,2}} \geq \frac{1}{2}.$$

As a consequence, the first derivative of  $V$  satisfies (3.24) for every  $t \geq 0$ .  $\square$

We now have all the ingredients to prove Theorem 2.

**3.5. Proof of Theorem 2.** Lemma 3.1 states that any solution to (1.6) starting from the set  $\mathcal{D}$  reaches  $\mathcal{K}_p$  after a finite time. Let us show that because of Lemma 3.2, any solution to (1.6) which starts from  $\mathcal{K}_p$  converges exponentially fast to  $(\zeta, 0, 0, \zeta)$  when  $t$  tends to infinity. To do this, we need to introduce some positive constants

$$C_2 := z_{min}^2 e^{-V(\mathbf{z}(0))}, \quad C_3 := \frac{2}{C_2} z_{max}$$

$$C_4 := \frac{z_{max}}{2} V(\mathbf{z}(0)), \quad C_5 := z(4b\beta - 2d + 3p)C_4,$$

where we recall that  $z_{min}$  and  $z_{max}$  have been defined in (3.11).

First, we prove that the population density differences  $z_{A,1} - z_{a,1}$  and  $z_{a,2} - z_{A,2}$  cannot be too small. To do this, we use the decay of the function  $V$  stated in Lemma 3.2:

$$\begin{aligned} V(\mathbf{z}(0)) \geq V(\mathbf{z}(t)) &= \ln \left( \frac{z_{A,1}(t) + z_{a,1}(t)}{z_{A,1}(t) - z_{a,1}(t)} \frac{z_{a,2}(t) + z_{A,2}(t)}{z_{a,2}(t) - z_{A,2}(t)} \right) \\ &\geq \ln \left( \frac{z_{min}^2}{(z_{A,1}(t) - z_{a,1}(t))(z_{a,2}(t) - z_{A,2}(t))} \right). \end{aligned}$$

This implies that

$$(3.27) \quad (z_{A,1}(t) - z_{a,1}(t))(z_{a,2}(t) - z_{A,2}(t)) \geq C_2.$$

Now, from the inequality  $\ln x \leq x - 1$  for  $x \geq 1$  we deduce for  $\mathbf{z}$  in  $\mathcal{K}_p$ ,

$$\begin{aligned} (3.28) \quad V(\mathbf{z}) &\leq \left( \frac{z_{A,1} + z_{a,1}}{z_{A,1} - z_{a,1}} - 1 \right) + \left( \frac{z_{a,2} + z_{A,2}}{z_{a,2} - z_{A,2}} - 1 \right) \\ &= 2 \frac{z_{a,1}(z_{a,2} - z_{A,2}) + z_{A,2}(z_{A,1} - z_{a,1})}{(z_{A,1} - z_{a,1})(z_{a,2} - z_{A,2})} \leq C_3(z_{a,1} + z_{A,2}), \end{aligned}$$



where we have used that  $z \in \mathcal{K}_p$  and inequality (3.27). Then combining (3.24) and (3.28), we get

$$(3.29) \quad \frac{d}{dt} V(\mathbf{z}(t)) \leq -\frac{C_1}{C_3} V(\mathbf{z}(t)),$$

which implies for every  $t \geq 0$ :

$$(3.30) \quad V(\mathbf{z}(t)) \leq V(\mathbf{z}(0))e^{-C_1 t/C_3}.$$

Now, from the inequality  $\ln x \geq (x-1)/x$  for  $x \geq 1$  we deduce for  $\mathbf{z}$  in  $\mathcal{K}_p$ ,

$$(3.31) \quad \begin{aligned} V(\mathbf{z}) &\geq \left( \frac{z_{A,1} + z_{a,1}}{z_{A,1} - z_{a,1}} - 1 \right) \frac{z_{A,1} - z_{a,1}}{z_{A,1} + z_{a,1}} + \left( \frac{z_{a,2} + z_{A,2}}{z_{a,2} - z_{A,2}} - 1 \right) \frac{z_{a,2} - z_{A,2}}{z_{a,2} + z_{A,2}} \\ &= \frac{2z_{a,1}}{z_{A,1} + z_{a,1}} + \frac{2z_{A,2}}{z_{a,2} + z_{A,2}} \geq \frac{2}{z_{\max}}(z_{a,1} + z_{A,2}). \end{aligned}$$

Hence,

$$(3.32) \quad z_{a,1}(t) + z_{A,2}(t) \leq C_4 e^{-C_1 t/C_3},$$

and the exponential convergence of  $z_{a,1}$  and  $z_{A,2}$  to 0 is proved. Let us now focus on the two other variables,  $z_{A,1}$  and  $z_{a,2}$ . From the definition of the dynamical system in (1.6), and noticing that  $|z_{A,1}(t) - \zeta| \leq \zeta$  as  $z \in \mathcal{K}_p$ , we get

$$\begin{aligned} \frac{d}{dt} (z_{A,1}(t) - \zeta)^2 &= -2cz_{A,1}(t)(z_{A,1}(t) - \zeta)^2 + 2pz_{a,2}(t)(z_{A,1}(t) - \zeta) \frac{z_{A,2}(t)}{z_{A,2}(t) + z_{a,2}} \\ &\quad - 2z_{a,1}(t)(z_{A,1}(t) - \zeta) \left( cz_{A,1}(t) + (p + b(\beta - 1)) \frac{z_{A,1}(t)}{z_{A,1}(t) + z_{a,1}(t)} \right) \\ &\leq -cz_{\min} (z_{A,1}(t) - \zeta)^2 + 2p\zeta z_{A,2}(t) + 2\zeta z_{a,1}(t) (cz_{\max} + p + b(\beta - 1)) \\ &\leq -cz_{\min} (z_{A,1}(t) - \zeta)^2 + \zeta(4b\beta - 2d + 3p)(z_{a,1}(t) + z_{A,2}(t)) \\ &\leq -cz_{\min} (z_{A,1}(t) - \zeta)^2 + C_5 e^{-C_1 t/C_3}. \end{aligned}$$

Hence, a classical comparison of nonnegative solutions of ordinary differential equations yields

$$(z_{A,1}(t) - \zeta)^2 \leq \left( (z_{A,1}(0) - \zeta)^2 - \frac{C_5}{cz_{\min} - C_1/C_3} \right) e^{-cz_{\min} t} + \frac{C_5}{cz_{\min} - C_1/C_3} e^{-C_1 t/C_3},$$

which gives the exponential convergence of  $z_{A,1}$  to  $\zeta$ . Reasoning similarly for the term  $z_{a,2}$  ends the proof of Theorem 2.

#### 4. STOCHASTIC PROCESS

In this section, we study properties of the stochastic process  $(\mathbf{N}^K(t), t \geq 0)$ . We derive an approximation for the extinction time of subpopulations under some small initial conditions, and then combine the results of this section with these on dynamical system (Section 3) to prove Theorem 3.

**4.1. Approximation of the extinction time.** Let us first study the stochastic system  $(\mathbf{Z}^K(t), t \geq 0)$  around the equilibrium  $(\zeta, 0, 0, \zeta)$  when  $K$  is large. The aim is to estimate the time before the loss of all  $a$ -individuals in the patch 1 and all  $A$ -individuals in the patch 2, which we denote by

$$(4.1) \quad T_0^K = \inf\{t \geq 0, Z_{a,1}^K(t) + Z_{A,2}^K(t) = 0\}.$$

Recall that  $\zeta = (b\beta - d)c^{-1} > 0$  and that the sequence of initial states  $(\mathbf{Z}^K(0), K \geq 1)$  converges in probability when  $K$  goes to infinity to a deterministic vector  $\mathbf{z}^0 = (z_{A,1}^0, z_{a,1}^0, z_{A,2}^0, z_{a,2}^0) \in \mathbb{R}_+^{\mathcal{E}}$ .

**Proposition 4.1.** *There exist two positive constants  $\varepsilon_0$  and  $C_0$  such that for any  $\varepsilon \leq \varepsilon_0$ , if there exists  $\eta \in ]0, 1/2[$  such that  $\max(|z_{A,1}^0 - \zeta|, |z_{A,2}^0 - \zeta|) \leq \varepsilon$  and  $\eta\varepsilon/2 \leq z_{a,1}^0, z_{A,2}^0 \leq \varepsilon/2$ , then*

$$\begin{aligned} \text{for any } C > (b(\beta - 1))^{-1} + C_0\varepsilon, \quad \mathbb{P}(T_0^K \leq C \log(K)) &\xrightarrow{K \rightarrow +\infty} 1, \\ \text{for any } 0 \leq C < (b(\beta - 1))^{-1} - C_0\varepsilon, \quad \mathbb{P}(T_0^K \leq C \log(K)) &\xrightarrow{K \rightarrow +\infty} 0. \end{aligned}$$

Remark that the upper bound on  $T_0^K$  still holds if  $z_{a,1}^0 = 0$  or  $z_{A,2}^0 = 0$ . Moreover, if  $z_{a,1}^0 = z_{A,2}^0 = 0$ , then the upper bound is satisfied with  $C_0 = 0$ . In the case where  $\eta = 0$ , the upper bound of the extinction time still holds but not the lower bound. Indeed, as the initial conditions  $z_{a,1}^0$  and  $z_{A,2}^0$  go to 0, the extinction time is faster.

*Proof.* The proof relies on several coupling arguments. Our first step is to prove that the population sizes  $Z_{A,1}^K$  and  $Z_{a,2}^K$  remain close to  $\zeta$  on a long time scale. In a second step, we couple the processes  $Z_{a,1}^K$  and  $Z_{A,2}^K$  with subcritical branching processes whose extinction times are known. We begin with introducing some additional notations: for any  $\gamma, \varepsilon > 0$  and  $(\alpha, i) \in \mathcal{E}$ ,

$$(4.2) \quad R_{\alpha,i}^{K,\gamma} = \inf\{t \geq 0, |Z_{\alpha,i}^K(t) - \zeta| \geq \gamma\},$$

and

$$(4.3) \quad T_{\alpha,i}^{K,\varepsilon} = \inf\{t \geq 0, Z_{\alpha,i}^K(t) \geq \varepsilon\}.$$

**Step 1:** The first step consists in proving that as long as the population processes  $Z_{a,1}^K$  and  $Z_{A,2}^K$  have small values, the processes  $Z_{A,1}^K$  and  $Z_{a,2}^K$  stay close to  $\zeta$ . To this aim, we study the system on the time interval

$$I_1^{K,\varepsilon} := \left[0, R_{A,1}^{K,\zeta/2} \wedge R_{a,2}^{K,\zeta/2} \wedge T_{a,1}^{K,\varepsilon} \wedge T_{A,2}^{K,\varepsilon}\right],$$

where  $a \wedge b$  stands for  $\min(a, b)$ .

Let us first bound the rates of the population process  $Z_{A,1}^K$ .

- We start with the birth rate of  $A$ -individuals in the patch 1. Let us remark that as  $\beta > 1$ , the ratio  $(\beta x + y)/(x + y) \leq \beta$  for any  $x, y \in \mathbb{R}_+$ . Moreover, the function  $x \mapsto (\beta x + y)/(x + y)$  increases with  $x$ , for any  $y \in \mathbb{R}_+$ . Combining these observations with the fact that for any  $t < T_{a,1}^{K,\varepsilon} \wedge R_{A,1}^{K,\zeta/2}$ ,  $0 \leq Z_{a,1}^K(t) \leq \varepsilon$  and  $Z_{A,1}^K(t) \geq \zeta/2$ , we deduce that the birth rate of  $A$ -individuals in the patch 1,  $K\tilde{\lambda}_{A,1}(\mathbf{Z}^K(t))$ , defined in (A.1) can be bounded:

$$b\beta \left(\frac{\zeta}{\zeta + 2\varepsilon}\right) K Z_{A,1}^K(t) \leq K\tilde{\lambda}_{A,1}(\mathbf{Z}^K(t)) \leq b\beta K Z_{A,1}^K(t).$$

- The migration rate of  $A$ -individuals from the patch 2 to the patch 1 is sandwiched as follows for any  $t < T_{a,1}^{K,\varepsilon} \wedge R_{A,1}^{K,\zeta/2}$ :

$$0 \leq K\tilde{\rho}_{2 \rightarrow 1}(\mathbf{Z}^K(t)) \leq Kp\varepsilon.$$

- The death rate of  $A$ -individuals in the patch 1 and the migration rate from patch 1 to patch 2 are bounded as follows:

$$(d + cZ_{A,1}^K(t)) K Z_{A,1}^K(t) \leq K\tilde{d}_{A,1}(\mathbf{Z}^K(t)) \leq (d + c\varepsilon + cZ_{A,1}^K(t)) K Z_{A,1}^K(t),$$

$$0 \leq K\tilde{\rho}_{1 \rightarrow 2}(\mathbf{Z}^K(t)) \leq Kp\varepsilon.$$

Hence, using an explicit construction of the process  $Z_{A,1}^K$  by means of Poisson point measures as in (1.5), we deduce that on the time interval  $I_1^{K,\varepsilon}$ ,  $Z_{A,1}^K$  is stochastically bounded by

$$\mathcal{Y}_{inf}^K \preceq Z_{A,1}^K \preceq \mathcal{Y}_{sup}^K,$$

where  $\mathcal{Y}_{inf}^K$  is a  $\mathbb{N}/K$ -valued Markov jump process with transition rates

$$\begin{aligned} & Kb\beta \left(1 - \frac{2\varepsilon}{\zeta + 2\varepsilon}\right) \frac{i}{K} \quad \text{from } \frac{i}{K} \text{ to } \frac{(i+1)}{K}, \\ & K \left( \left(d + c\varepsilon + c\frac{i}{K}\right) \frac{i}{K} + p\varepsilon \right) \quad \text{from } \frac{i}{K} \text{ to } \frac{(i-1)}{K}, \end{aligned}$$

and initial value  $Z_{A,1}^K(0)$ , and  $\mathcal{Y}_{sup}^K$  is a  $\mathbb{N}/K$ -valued Markov jump process with transition rates

$$\begin{aligned} & K \left( b\beta \frac{i}{K} + p\varepsilon \right) \quad \text{from } \frac{i}{K} \text{ to } \frac{(i+1)}{K}, \\ & K \left( d + c\frac{i}{K} \right) \frac{i}{K} \quad \text{from } \frac{i}{K} \text{ to } \frac{(i-1)}{K}. \end{aligned}$$

and initial value  $Z_{A,1}^K(0)$ .

Let us focus on the process  $\mathcal{Y}_{inf}^K$ . Using a proof similar to the one of Lemma 1.1, we prove that since the sequence  $(\mathcal{Y}_{inf}^K(0), K \geq 1)$  converges in probability to the deterministic value  $z_{A,1}^0$ ,

$$\lim_{K \rightarrow +\infty} \sup_{s \leq t} |\mathcal{Y}_{inf}^K(s) - \Phi_{inf}(s)| = 0 \quad a.s$$

for every finite time  $t > 0$ , where  $\Phi_{inf}$  is the solution to

$$(4.4) \quad \Phi'(t) = b\beta(1 - 2\varepsilon/(\zeta + 2\varepsilon))\Phi(t) - p\varepsilon - (d + c\varepsilon + c\Phi(t))\Phi(t)$$

with initial value  $z_{A,1}^0$ . Let us study the trajectory of  $\Phi_{inf}$ . The polynomial in  $\Phi(t)$  on the r.h.s. of (4.4) has two roots

$$\begin{aligned} (4.5) \quad \Phi_{inf}^\pm &= \frac{1}{2c} \left( b\beta \left(1 - \frac{2\varepsilon}{\zeta + 2\varepsilon}\right) - d - c\varepsilon \pm \sqrt{\left(b\beta \left(1 - \frac{2\varepsilon}{\zeta + 2\varepsilon}\right) - d - c\varepsilon\right)^2 - 4pc\varepsilon} \right) \\ &= \frac{\zeta}{2} - \frac{\varepsilon}{2} \left( \frac{2b\beta}{(\zeta + 2\varepsilon)c} + 1 \right) \pm \sqrt{\left( \frac{\zeta}{2} - \frac{\varepsilon}{2} \left( \frac{2b\beta}{(\zeta + 2\varepsilon)c} + 1 \right) \right)^2 - \frac{p\varepsilon}{c}}. \end{aligned}$$

As a consequence,  $\Phi' > 0$  if and only if  $\Phi \in ]\Phi_{inf}^-, \Phi_{inf}^+]$ . Definition (4.5) implies that for small  $\varepsilon$ ,

$$\Phi_{inf}^- \sim pc\varepsilon.$$

Hence, if  $\varepsilon_0$  is chosen sufficiently small and for any  $\varepsilon < \varepsilon_0$ ,

$$\Phi_{inf}^- \leq 2pc\varepsilon_0 < z_{A,1}^0.$$

Thus, we observe that any solution to (4.4) with initial condition  $\Phi_{inf}(0) \in [2pc\varepsilon_0, +\infty[$  is monotonous and converges to  $\Phi_{inf}^+$ . Similarly, we obtain that if  $\varepsilon_0$  is sufficiently small, then there exists  $M' > 0$  such that for any  $\varepsilon < \varepsilon_0$ ,  $|\Phi_{inf}^+ - \zeta| \leq M'\varepsilon$ . We define the stopping time

$$R_{\mathcal{Y}_{inf}^K}^{K,M'} = \inf \{ t \geq 0, \mathcal{Y}_{inf}^K \notin [\zeta - (M' + 1)\varepsilon, \zeta + (M' + 1)\varepsilon] \}.$$

As in the proof of Theorem 3/(c) in [9], we can construct a family of Markov jump processes  $\tilde{\mathcal{Y}}_{inf}^K$  with transition rates that are positive, bounded, Lipschitz and uniformly bounded away

from 0, for which we can find the following estimate (Chapter 5 of Freidlin and Wentzell [20]): there exists  $V' > 0$  such that,

$$\mathbb{P}(R_{\mathcal{Y}_{inf}^K}^{K,M'} > e^{KV'}) = \mathbb{P}(R_{\mathcal{Y}_{inf}^K}^{K,M'} > e^{KV'}) \xrightarrow{K \rightarrow +\infty} 1.$$

We can deal with the process  $\mathcal{Y}_{sup}^K$  similarly and find  $M'' > 0$  and  $V'' > 0$  such that

$$\mathbb{P}(R_{\mathcal{Y}_{sup}^K}^{K,M''} > e^{KV''}) \xrightarrow{K \rightarrow +\infty} 1,$$

with

$$R_{\mathcal{Y}_{sup}^K}^{K,M''} = \inf \left\{ t \geq 0, \mathcal{Y}_{sup}^K(t) \notin [\zeta - (M'' + 1)\varepsilon, \zeta + (M'' + 1)\varepsilon] \right\}.$$

Finally, for  $M_1 = M' \vee M''$  and  $V_1 = V' \wedge V''$ , we deduce that  $\mathbb{P}(R_{\mathcal{Y}_{inf}^K}^{K,M_1} \wedge R_{\mathcal{Y}_{sup}^K}^{K,M_1} > e^{KV_1}) \xrightarrow{K \rightarrow +\infty} 1$ .

1. Moreover, if  $R_{A,1}^{K,(M_1+1)\varepsilon} \leq R_{A,1}^{K,\zeta/2} \wedge R_{a,2}^{K,\zeta/2} \wedge T_{a,1}^{K,\varepsilon} \wedge T_{A,2}^{K,\varepsilon}$ , then

$$R_{A,1}^{K,(M_1+1)\varepsilon} \geq R_{\mathcal{Y}_{inf}^K}^K \wedge R_{\mathcal{Y}_{sup}^K}^K.$$

Thus

$$(4.6) \quad \mathbb{P}(R_{A,1}^{K,\zeta/2} \wedge R_{a,2}^{K,\zeta/2} \wedge T_{a,1}^{K,\varepsilon} \wedge T_{A,2}^{K,\varepsilon} \wedge e^{KV_1} > R_{A,1}^{K,(M_1+1)\varepsilon}) \xrightarrow{K \rightarrow +\infty} 0.$$

Using symmetrical arguments for the population process  $Z_{a,2}^K$ , we find  $M_2 > 0$  and  $V_2 > 0$  such that

$$(4.7) \quad \mathbb{P}(R_{A,1}^{K,\zeta/2} \wedge R_{a,2}^{K,\zeta/2} \wedge T_{a,1}^{K,\varepsilon} \wedge T_{A,2}^{K,\varepsilon} \wedge e^{KV_2} > R_{a,2}^{K,(M_2+1)\varepsilon}) \xrightarrow{K \rightarrow +\infty} 0.$$

Finally, we set  $M = M_1 \vee M_2$  and  $V = V_1 \wedge V_2$ . Limits (4.6) and (4.7) are still true with  $M$  and  $V$ . Thus we have proved that, as long as the size of the  $a$ -population in Patch 1 and the size of the  $A$ -population in Patch 2 are small and as long as the time is smaller than  $e^{KV}$ , the processes  $Z_{A,1}^K$  and  $Z_{a,2}^K$  stay close to  $\zeta$ , i.e. they belong to  $[\zeta - (M+1)\varepsilon, \zeta + (M+1)\varepsilon]$ .

Note that if  $\varepsilon_0$  is sufficiently small,  $R_{A,1}^{K,(M+1)\varepsilon} \leq R_{A,1}^{K,\zeta/2}$  and  $R_{a,2}^{K,(M+1)\varepsilon} \leq R_{a,2}^{K,\zeta/2}$  a.s. for all  $\varepsilon < \varepsilon_0$ . So we reduce our study to the time interval

$$I_2^{K,\varepsilon} := \left[ 0, R_{A,1}^{K,(M+1)\varepsilon} \wedge R_{a,2}^{K,(M+1)\varepsilon} \wedge T_{a,1}^{K,\varepsilon} \wedge T_{A,2}^{K,\varepsilon} \right].$$

**Step 2:** In the sequel we study the extinction time of the stochastic processes  $(Z_{a,1}^K(t), t \geq 0)$  and  $(Z_{A,2}^K(t), t \geq 0)$ . We recall that there exists  $\eta \in ]0, 1/2[$  such that  $\eta\varepsilon/2 \leq z_{a,1}^0, z_{A,2}^0 \leq \varepsilon/2$ . Bounding the birth and death rates of  $(Z_{a,1}^K(t), t \geq 0)$  and  $(Z_{A,2}^K(t), t \geq 0)$  as previously, we deduce that the sum  $(Z_{a,1}^K(t) + Z_{A,2}^K(t), t \geq 0)$  is stochastically bounded as follows, on the time interval  $I_2^{K,\varepsilon}$ :

$$\frac{\mathcal{N}_{inf}^K}{K} \preceq Z_{a,1}^K + Z_{A,2}^K \preceq \frac{\mathcal{N}_{sup}^K}{K}.$$

where  $\mathcal{N}_{inf}^K$  is a  $\mathbb{N}$ -valued binary branching process with birth rate  $b + p \frac{\zeta - (M+1)\varepsilon}{\zeta - M\varepsilon}$ , death rate  $d + c\zeta + c(M+2)\varepsilon + p$  and initial state  $\lfloor \eta\varepsilon K \rfloor$ , and  $\mathcal{N}_{sup}^K$  is a  $\mathbb{N}$ -valued binary branching process with birth rate

$$b \frac{\zeta + \varepsilon(\beta - M - 1)}{\zeta - M\varepsilon} + p,$$

death rate

$$d + c\zeta - c(M+1)\varepsilon + p \frac{\zeta - (M+1)\varepsilon}{\zeta - M\varepsilon},$$

and initial state  $\lfloor \varepsilon K \rfloor + 1$ .

It remains to estimate the extinction time for a binary branching process  $(\mathcal{N}_t, t \geq 0)$  with a birth rate  $B$  and a death rate  $D > B$ . Applying (A.2) with  $i = \lfloor \eta \varepsilon K \rfloor$ , we get:

$$\begin{aligned} \forall C < (D - B)^{-1}, \quad \mathbb{P}(S_0^{\mathcal{N}} \leq C \log(K)) &\xrightarrow{K \rightarrow +\infty} 0, \\ \forall C > (D - B)^{-1}, \quad \mathbb{P}(S_0^{\mathcal{N}} \leq C \log(K)) &\xrightarrow{K \rightarrow +\infty} 1. \end{aligned}$$

Moreover, if

$$S_{\lfloor \varepsilon K \rfloor}^{\mathcal{N}} := \inf\{t > 0, \mathcal{N}(t) \geq \lfloor \varepsilon K \rfloor\},$$

then

$$(4.8) \quad \mathbb{P}\left(S_0^{\mathcal{N}} > K \wedge S_{\lfloor \varepsilon K \rfloor}^{\mathcal{N}}\right) \xrightarrow{K \rightarrow +\infty} 0$$

(cf. Theorem 4 in [9]). Thus

$$\begin{aligned} \mathbb{P}(T_0^K < C \log(K)) &- \mathbb{P}\left(S_0^{\mathcal{N}_{inf}^K} < C \log(K)\right) \\ &\leq \mathbb{P}\left(T_0^K > T_{a,1}^{K,\varepsilon} \wedge T_{A,2}^{K,\varepsilon} \wedge K\right) + \mathbb{P}\left(T_{a,1}^{K,\varepsilon} \wedge T_{A,2}^{K,\varepsilon} \wedge K > R_{A,1}^{K,(M+1)\varepsilon} \wedge R_{a,2}^{K,(M+1)\varepsilon}\right) \\ &\leq \mathbb{P}\left(S_0^{\mathcal{N}_{sup}^K} > S_{\lfloor \varepsilon K \rfloor}^{\mathcal{N}_{sup}^K} \wedge K\right) + \mathbb{P}\left(T_{a,1}^{K,\varepsilon} \wedge T_{A,2}^{K,\varepsilon} \wedge K > R_{A,1}^{K,(M+1)\varepsilon} \wedge R_{a,2}^{K,(M+1)\varepsilon}\right). \end{aligned}$$

The last term of the last line converges to 0 when  $K$  tends to 0 according to (4.6) and (4.7). The first one also tends to 0 according to (4.8). Thus,

$$\lim_{K \rightarrow +\infty} \mathbb{P}(T_0^K < C \log(K)) \leq \lim_{K \rightarrow +\infty} \mathbb{P}\left(S_0^{\mathcal{N}_{inf}^K} < C \log(K)\right).$$

We prove similarly that

$$\lim_{K \rightarrow +\infty} \mathbb{P}(T_0^K < C \log(K)) \geq \lim_{K \rightarrow +\infty} \mathbb{P}\left(S_0^{\mathcal{N}_{sup}^K} < C \log(K)\right).$$

We conclude the proof by noticing that the growth rates of the processes  $\mathcal{N}_{inf}^K$  and  $\mathcal{N}_{sup}^K$  are equal to  $-b(\beta - 1)$  up to a constant times  $\varepsilon$ .  $\square$

**4.2. Proof of Theorem 3.** We can now prove our main result:

Let  $\varepsilon$  be a small positive number. Applying Lemma 1.1 and Theorem 1 we get the existence of a positive real number  $s_\varepsilon$  such that

$$\lim_{K \rightarrow \infty} \mathbb{P}(\|\mathbf{N}^K(s_\varepsilon) - (\zeta K, 0, 0, \zeta K)\| \leq \varepsilon K/2) = 1.$$

Using Proposition 4.1 and the Markov property yield that there exists  $C_0 > 0$  such that

$$\lim_{K \rightarrow \infty} \mathbb{P}\left(\left|\frac{T_{\mathcal{B}_\varepsilon}^K}{\log K} - \frac{1}{b(\beta - 1)}\right| \leq C_0 \varepsilon\right) = 1,$$

where by definition, we recall that  $T_{\mathcal{B}_\varepsilon}^K$  is the hitting time of  $\mathcal{B}_\varepsilon$ . Moreover, the migration rates are equal to zero for any  $t \geq T_{\mathcal{B}_\varepsilon}^K$ , so

$$Z_{a,1}^K(t) = Z_{A,2}^K(t) = 0, \quad \text{for any } t \geq T_{\mathcal{B}_\varepsilon}^K.$$

After the time  $T_{\mathcal{B}_\varepsilon}^K$ , the  $A$ -population in the patch 1 and the  $a$ -population in the patch 2 evolve independently from each other according to two logistic birth and death processes with

birth rate  $b\beta$ , death rate  $d$  and competition rate  $c$ . Using Theorem 3(c) in Champagnat [9], we deduce that for any  $m > 1$ , there exists  $V > 0$  such that

$$\inf_{X \in \mathcal{B}_\varepsilon} \mathbb{P}_X(T_{\mathcal{B}_{m\varepsilon}}^K \geq e^{KV}) \xrightarrow{K \rightarrow +\infty} 1,$$

which ends the proof.

## 5. INFLUENCE OF THE MIGRATION PARAMETER $p$ : NUMERICAL SIMULATIONS

In this section, we present some simulations of the deterministic dynamical system (1.6). We are concerned with the influence of the migration rate  $p$  on the time to reach a neighbourhood of the equilibrium (1.11). Note that  $p$  has no impact on the corresponding relaxation time for the stochastic system, because extinction of the minorities happens on a longer time scale.

For any value of  $p$ , we evaluate the first time  $T_\varepsilon(p)$  such that the solution  $(z_{A,1}(t), z_{a,1}(t), z_{A,2}(t), z_{a,2}(t))$  to (1.6) belongs to the set

$$\mathcal{S}_\varepsilon = \{(z_{A,1}, z_{a,1}, z_{A,2}, z_{a,2}) \in \mathbb{R}_+^4, (z_{A,1} - \zeta)^2 + z_{a,1}^2 + z_{A,2}^2 + (z_{a,2} - \zeta)^2 \leq \varepsilon^2\},$$

which corresponds to the first time the solution enters an  $\varepsilon$ -neighbourhood of  $(\zeta, 0, 0, \zeta)$ .

In the following simulations, the demographic parameters are given by:

$$\beta = 2, \quad b = 2, \quad d = 1 \quad \text{and} \quad c = 0.1.$$

For these parameters,

$$\zeta = 30 \quad \text{and} \quad p_0 = \sqrt{5} - 1 \simeq 1.24.$$

The migration rate as well as the initial condition vary.

**Description of the figures:** Figure 2 presents the plots of  $p \mapsto T_\varepsilon(p) - T_\varepsilon(0)$ . The simulations are computed with  $\varepsilon = 0.01$  and with initial conditions  $(z_{A,1}(0), z_{a,1}(0), z_{A,2}(0), z_{a,2}(0))$  such that  $z_{a,1}(0) = z_{A,1}(0) - 0.1$  with  $z_{A,1}(0) \in \{0.3, 0.5, 1, 2, 3, 5, 10, 15\}$  and  $(z_{A,2}(0), z_{a,2}(0)) \in \{(1, 30), (15, 16)\}$ . Figure 3 presents the trajectories of some solutions to the dynamical system (1.6) in the two phase planes which represent the two patches. We use the same parameters as in Figure 2 and the initial conditions are given in the captions. For each initial condition, we plot the trajectories for three different values of  $p$ : 0, 1 and 20.

**Conjecture:** First of all, we observe that for all values under consideration, the time  $T_\varepsilon(p)$  to reach the set  $\mathcal{S}_\varepsilon$  is finite even if  $p > p_0$ . Therefore, we make the following conjecture:

**Conjecture 1.** *For any initial condition  $(z_{1,A}(0), z_{1,a}(0), z_{2,A}(0), z_{2,a}(0)) \in \mathcal{D}$ , where  $\mathcal{D}$  is defined by (1.16),*

$$(z_{1,A}(t), z_{1,a}(t), z_{2,A}(t), z_{2,a}(t)) \xrightarrow{t \rightarrow +\infty} (\zeta, 0, 0, \zeta).$$

**Influence of  $p$  when the initial condition in patch 2 is close to the equilibrium:**

Figure 2(a) presents the results for  $(z_{A,2}(0), z_{a,2}(0)) = (1, 30)$ , that is if the initial condition in the patch 2 is close to its equilibrium (recall that  $\zeta = 30$  with the parameters under study). Observe that for any value of  $(z_{A,1}(0), z_{a,1}(0) = z_{A,1}(0) - 0.1)$ , the time for reproductive isolation to occur is reduced when the migration rate is large. Hence, the migration rate seems here to strengthen the homogeneity. This is confirmed by Figure 3(a) and (b) where examples of trajectories with the same initial conditions as in Figure 2(a) are drawn. The two Figures 3(a) and (b) present similar behaviours: when  $p$  increases, the number of  $a$ -individuals in patch 1 decreases at any time whereas the number and the proportion of  $a$ -individuals in patch 2 remain almost constant. These behaviours derive from two phenomena. On the one hand, the  $a$ -individuals are able to leave patch 1 faster when  $p$  is large. On the other hand, the value of  $p$  does not affect the migration outside patch 2 which is almost zero in view of

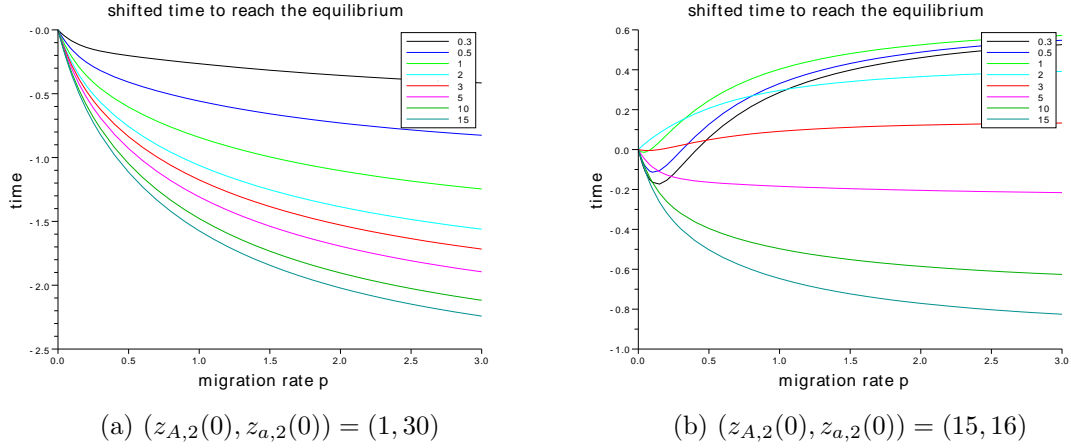


FIGURE 2. For different values of the initial condition, we plot  $p \mapsto T_\varepsilon(p) - T_\varepsilon(0)$ . The initial condition is  $(z_{A,1}(0), z_{A,1}(0) - 0.1, z_{A,2}(0), z_{a,2}(0))$  where  $z_{A,1}(0) \in \{0.3, 0.5, 1, 2, 3, 5, 10, 15\}$  as represented by the colors of the legend; and  $(z_{A,2}(0), z_{a,2}(0)) = (1, 30)$  on the left, and  $(z_{A,2}(0), z_{a,2}(0)) = (15, 16)$  on the right.

the small proportion of  $A$ -individuals in the patch 2.

#### Influence of $p$ when $a$ - and $A$ -population sizes are initially similar in patch 2:

On Figure 2(b) we are interested in the case where the  $A$ - and  $a$ - initial populations in patch 2 have a similar size and the sum  $z_{A,2}(0) + z_{a,2}(0)$  is close to  $\zeta$ . Observe that for  $z_{A,1}(0) \in \{5, 10, 15\}$ , the time  $T_\varepsilon(p)$  decreases with respect to  $p$  but not as fast as previously. By plotting some trajectories when  $z_{A,1}(0) = 10$  on Figure 3(c), we note that the dynamics is not the same as for the previous case (Fig. 3(a)). Here, a large migration rate affects the migration outside the two patches in such a way that the equilibrium is reached faster. Finally, Figure 2(b) also presents behaviours that are essentially different for  $z_{A,1}(0) \in \{0.3, 0.5, 1, 2, 3\}$ . In these cases, the migration rate does not strengthen the homogamy. We plot some trajectories from this latter case in Figure 3(d) where  $z_{A,1}(0) = 1$ . Observe that a high value of  $p$  favors the migration outside patch 2 for the two types  $a$  and  $A$  since the proportions of the two alleles in patch 2 are almost equal at time  $t = 0$ . This is not the case in the patch 1 where the value of  $p$  does not affect significantly the initial migration outside patch 1 since the population sizes are smaller. Hence, patch 1 is filled by the individuals that flee patch 2 where the migration rate is high. Therefore, both  $a$ - and  $A$ - populations increase at first, but the  $A$ -individuals remain dominant in patch 1 and thus the  $a$ -population is disadvantaged. Finally, the  $a$ -individuals that flee the patch 2, find a less favorable environment in patch 1 and therefore the time needed to reach the equilibrium is extended because of the dynamics in patch 1.

As a conclusion, similarly to the case of selection-migration model (see e.g. [1]) migration can have different impacts on the population dynamics. On the one hand, a large migration rate helps the individuals to escape a disadvantageous habitat [12] but there are also risks to move through unfamiliar or less suitable habitat. Thus, a trade-off between the two phenomena explains the influence of  $p$  on the time to reach the equilibrium.

## 6. GENERALISATIONS OF THE MODEL

Until now we studied a simple model to make clear the important properties allowing to get spatial segregation between patches. We now prove that our findings are robust by studying

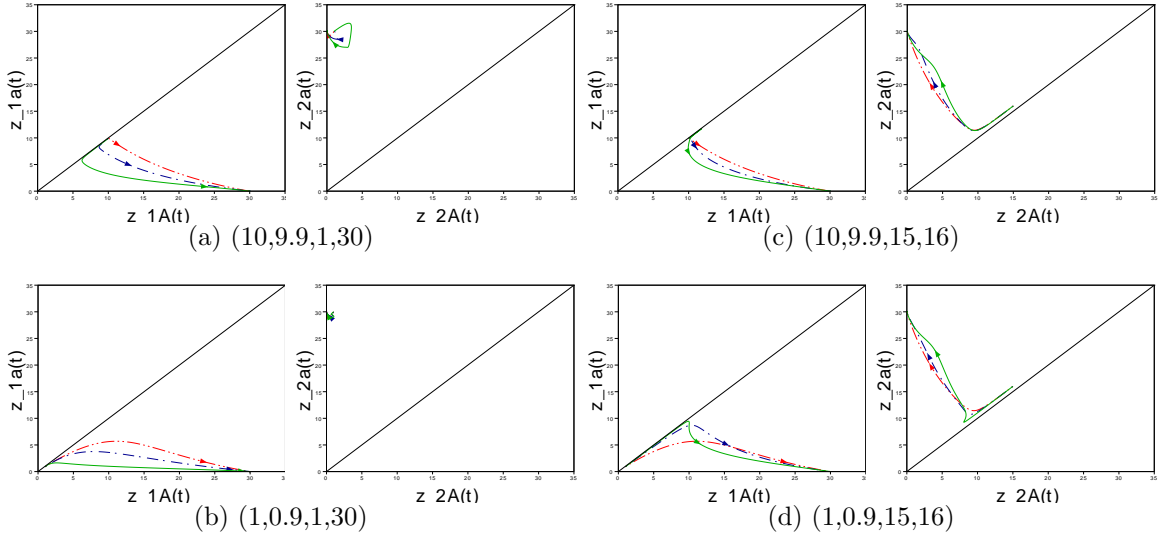


FIGURE 3. For four different initial conditions, we plot the trajectories in the phase planes which represent the patch 1 (left) and the patch 2 (right) for  $t \in [0, 10]$  and for three values of  $p$ :  $p = 0$  (red),  $p = 1$  (blue),  $p = 20$  (green). The initial condition is given under each pair of plots in the format  $(z_{A,1}(0), z_{a,1}(0), z_{A,2}(0), z_{a,2}(0))$ . Note that the initial conditions on (a) and (c) (resp. (b) and (d)) corresponds to the dark green (resp. light green) curve on Figure 2(a) and 2(b).

some generalisations of the model and showing that we can relax several assumptions and still get spatial segregation between patches.

**6.1. Differences between patches.** We assumed that the patches were ecologically equivalent in the sense that the birth, death and competition rates  $b$ ,  $d$  and  $c$ , respectively, did not depend on the label of the patch  $i \in \mathcal{I}$ . In fact we could make these parameters depend on the patch, and denote them  $b_i$ ,  $d_i$  and  $c_i$ ,  $i \in \mathcal{I}$ . In the same way, the sexual preference  $\beta_i$  and the migration rate  $p_i$  could depend on the label of the patch  $i \in \mathcal{I}$ . As a consequence, the dynamical system (1.6) becomes

$$(6.1) \quad \begin{cases} \frac{d}{dt} z_{A,1}(t) = z_{A,1} \left[ b_1 \frac{\beta_1 z_{A,1} + z_{a,1}}{z_{A,1} + z_{a,1}} - d_1 - c_1(z_{A,1} + z_{a,1}) - p_1 \frac{z_{a,1}}{z_{A,1} + z_{a,1}} \right] + p_2 \frac{z_{A,2} z_{a,2}}{z_{A,2} + z_{a,2}} \\ \frac{d}{dt} z_{a,1}(t) = z_{a,1} \left[ b_1 \frac{\beta_1 z_{a,1} + z_{A,1}}{z_{A,1} + z_{a,1}} - d_1 - c_1(z_{A,1} + z_{a,1}) - p_1 \frac{z_{A,1}}{z_{A,1} + z_{a,1}} \right] + p_2 \frac{z_{A,2} z_{a,2}}{z_{A,2} + z_{a,2}} \\ \frac{d}{dt} z_{A,2}(t) = z_{A,2} \left[ b_2 \frac{\beta_2 z_{A,2} + z_{a,2}}{z_{A,2} + z_{a,2}} - d_2 - c_2(z_{A,2} + z_{a,2}) - p_2 \frac{z_{a,2}}{z_{A,2} + z_{a,2}} \right] + p_1 \frac{z_{A,1} z_{a,1}}{z_{A,1} + z_{a,1}} \\ \frac{d}{dt} z_{a,2}(t) = z_{a,2} \left[ b_2 \frac{\beta_2 z_{a,2} + z_{A,2}}{z_{A,2} + z_{a,2}} - d_2 - c_2(z_{A,2} + z_{a,2}) - p_2 \frac{z_{A,2}}{z_{A,2} + z_{a,2}} \right] + p_1 \frac{z_{A,1} z_{a,1}}{z_{A,1} + z_{a,1}}. \end{cases}$$

The set  $\mathcal{D}$  is still invariant under this new system and the solutions to (6.1) with initial conditions in  $\mathcal{D}$  hit in finite time the invariant set

$$\mathcal{K}'_p := \left\{ \mathbf{z} \in \mathcal{D}, z_{A,i} + z_{a,i} \in \left[ \frac{b_i(\beta_i + 1) - 2d_i - p_i}{2c_i}, \zeta_i + \frac{p_i}{2c_i}, i \in \mathcal{I} \right] \right\},$$

where

$$\zeta_i := \frac{b_i \beta_i - d_i}{c_i}.$$

As  $\mathcal{D}$  is an invariant set under (6.1), we can define the function  $V$  as in (3.22) for every solution of  $V$  with initial condition in  $\mathcal{D}$ . Its first order derivative is

$$\frac{d}{dt} V(\mathbf{z}(t)) = - \sum_{i=1,2} \frac{z_{A,i} z_{a,i}}{z_{A,i} + z_{a,i}} \left[ \frac{2b_i(\beta_i - 1) + 2p_i}{z_{A,i} + z_{a,i}} - \frac{2p_i}{z_{A,\bar{i}} + z_{a,\bar{i}}} \right].$$



As a consequence, we can prove similar results to Theorems 2 and 3 under the assumption that  $p_1$  and  $p_2$  satisfy

$$p_i c_i (2c_i \zeta_i + p_i) < c_i (b_i (\beta_i - 1) + p_i) (b_i (\beta_i + 1) - 2d_i - p_i), \text{ for } i \in \mathcal{I},$$

and where the constant in front of the time  $\log K$  is no more  $\frac{1}{b(\beta-1)}$  but  $\frac{1}{\omega_{1,2}}$  with

$$\omega_{1,2} = \frac{1}{2} (b_1 (\beta_1 - 1) + p_1 + b_2 (\beta_2 - 1) + p_2) - \frac{1}{2} \sqrt{(b_1 (\beta_1 - 1) + p_1 - b_2 (\beta_2 - 1) - p_2)^2 + 4p_1 p_2}.$$

Here, note that the constant does depend on all the parameters. Indeed, since there is no ecological neutrality between the two patches, there do not exist simplifications and balancings as in the previous models.

**6.2. Migration.** The migration rates under consideration increase when the genetic diversity increases. Indeed, let us consider

$$H_T^{(i)} := 1 - \left[ \left( \frac{n_{A,i}}{n_{A,i} + n_{a,i}} \right)^2 + \left( \frac{n_{a,i}}{n_{A,i} + n_{a,i}} \right)^2 \right]$$

as a measure of the genetic diversity in the patch  $i \in \mathcal{I}$ . Note that  $H_T^{(i)} \in [0, 1/2]$  is known as the "total gene diversity" in the patch  $i$  (see [41] for instance) and is widely used as a measure of diversity. When we express the migration rates in terms of this measure, we get

$$\rho_{\alpha, \bar{i} \rightarrow i}(n) = p \frac{n_{A,i} n_{a,i}}{n_{A,i} + n_{a,i}} = \frac{p}{2} (n_{A,i} + n_{a,i}) H_T^{(i)}.$$

Hence we can consider that the migration helps the speciation. Let us show that we can get the same kind of result when we consider an arbitrary form for the migration rate if this latter is symmetrical and bounded. We thus consider a more general form for the migration rate. More precisely,

$$\rho_{\alpha, \bar{i} \rightarrow i}(n) = p(n_{A,\bar{i}}, n_{a,\bar{i}}),$$

and we assume

$$p(n_{A,\bar{i}}, n_{a,\bar{i}}) = p(n_{a,\bar{i}}, n_{A,\bar{i}}) \quad \text{and} \quad p(n_{A,\bar{i}}, n_{a,\bar{i}}) \frac{n_{A,\bar{i}} + n_{a,\bar{i}}}{n_{A,\bar{i}} n_{a,\bar{i}}} < p_0,$$

where  $p_0$  has been defined in (1.17). Note that the second condition on the function  $p$  imposes that as one of the population sizes goes to 0, then so does the migration rate. In particular, this condition ensures that the points given by (1.11) and (1.12) are still equilibria of the system. Theorems 2 and 3 still hold with this new definition for the migration rate.

**6.3. Number of patches.** Finally, we restricted our attention to the case of two patches, but we can consider an arbitrary number  $N \in \mathbb{N}$  of patches. We assume that all the patches are ecologically equivalent but that the migrant individuals have a probability to migrate to an other patch which depends on the geometry of the system. Moreover, we allow the individuals to migrate outside the  $N$  patches. In other words, for  $\alpha \in \mathcal{A}$ ,  $i \leq N$ ,  $j \leq N+1$  and  $\mathbf{n} \in (\mathbb{N}^{\mathcal{A}})^N$ ,

$$\rho_{\alpha, i \rightarrow j}(\mathbf{n}) = p_{ij} \frac{n_{A,i} n_{a,i}}{n_{A,i} + n_{a,i}},$$

where the "patch"  $N+1$  denotes the outside of the system.

As a consequence, we obtain the following limiting dynamical system for the rescaled process, when the initial population sizes are of order  $K$  in all the patches: for every  $1 \leq i \leq N$ ,

$$\begin{aligned}
(6.2) \quad \frac{dz_{A,i}(t)}{dt} &= z_{A,i} \left[ b \frac{\beta z_{A,i} + z_{a,i}}{z_{A,i} + z_{a,i}} - d - c(z_{A,i} + z_{a,i}) - \sum_{j \neq i, j \leq N+1} p_{ij} \frac{z_{a,i}}{z_{A,i} + z_{a,i}} \right] \\
&\quad + \sum_{j \neq i, j \leq N} p_{ji} \frac{z_{A,j} z_{a,j}}{z_{A,j} + z_{a,j}} \\
\frac{dz_{a,i}(t)}{dt} &= z_{a,i} \left[ b \frac{\beta z_{a,i} + z_{A,i}}{z_{A,i} + z_{a,i}} - d - c(z_{A,i} + z_{a,i}) - \sum_{j \neq i, j \leq N+1} p_{ij} \frac{z_{A,i}}{z_{A,i} + z_{a,i}} \right] \\
&\quad + \sum_{j \neq i, j \leq N} p_{ji} \frac{z_{A,j} z_{a,j}}{z_{A,j} + z_{a,j}}
\end{aligned}$$

For the sake of readability, we introduce the two following notations:

$$p_{i \rightarrow} := \sum_{j \neq i, j \leq N+1} p_{ij} \quad \text{and} \quad p_{i \leftarrow} := \sum_{j \neq i, j \leq N} p_{ji}.$$

Let  $N_A$  be an integer smaller than  $N$  which gives the number of patches with a majority of individuals of type  $A$ . We can assume without loss of generality that

$$z_{A,i}(0) > z_{a,i}(0), \text{ for } 1 \leq i \leq N_A, \quad \text{and} \quad z_{A,i}(0) < z_{a,i}(0), \text{ for } N_A + 1 \leq i \leq N.$$

Let us introduce the subset of  $(\mathbb{R}_+^A)^N$

$$\mathcal{D}_{N_A, N} := \{\mathbf{z} \in (\mathbb{R}_+^A)^N, z_{A,i} - z_{a,i} > 0 \text{ for } i \leq N_A, \text{ and } z_{a,i} - z_{A,i} > 0 \text{ for } i > N_A\},$$

We assume that the sequence  $(p_{ij})_{i,j \in \{1, \dots, N\}}$  satisfy : for all  $i \in \{1, \dots, N\}$ ,

$$(6.3) \quad p_{i \rightarrow} < b(\beta + 1) - 2d \quad \text{and} \quad \frac{b(\beta - 1) + p_{i \rightarrow}}{2cz + p_{i \leftarrow}} - \sum_{j \neq i, j \leq N+1} \frac{p_{ij}}{b(\beta + 1) - 2d - p_{j \rightarrow}} > 0.$$

Then we have the following result:

**Theorem 4.** *We assume that Assumption (6.3) holds. Let us assume that  $\mathbf{Z}^K(0)$  converges in probability to a deterministic vector  $\mathbf{z}^0$  belonging to  $\mathcal{D}_{N_A, N}$  with  $(z_{a,1}^0, z_{A,2}^0) \neq (0, 0)$ . Introduce the following bounded set depending on  $\varepsilon > 0$ :*

$$\mathcal{B}_{N_A, N, \varepsilon} := \left( [(\zeta - \varepsilon)K, (\zeta + \varepsilon)K] \times \{0\} \right)^{N_A} \times \left( \{0\} \times [(\zeta - \varepsilon)K, (\zeta + \varepsilon)K] \right)^{N - N_A}.$$

*Then there exist three positive constants  $\varepsilon_0$ ,  $C_0$  and  $m$ , and a positive constant  $V$  depending on  $(m, \varepsilon_0)$  such that if  $\varepsilon \leq \varepsilon_0$ ,*

$$\lim_{K \rightarrow \infty} \mathbb{P} \left( \left| \frac{T_{\mathcal{B}_\varepsilon}^K}{\log K} - \frac{1}{b(\beta - 1)} \right| \leq C_0 \varepsilon, \mathbf{N}^K \left( T_{\mathcal{B}_{N_A, N, \varepsilon}}^K + t \right) \in \mathcal{B}_{N_A, N, m\varepsilon} \forall t \leq e^{VK} \right) = 1,$$

*where  $T_{\mathcal{B}}^K$ ,  $\mathcal{B} \subset \mathbb{R}_+^\varepsilon$  is the hitting time of the set  $\mathcal{B}$  by the population process  $\mathbf{N}^K$ .*

The proof is really similar to the one for the two patches. To handle the deterministic part of the proof, we first show that for every initial condition on  $\mathcal{D}_{N_A, N}$ , the solution of (6.2) hits the set

$$\mathcal{K}_{N_A, N} := \left\{ \mathbf{z} \in \left( (\mathbb{R}_+^*)^A \right)^N, \{z_{A,i} + z_{a,i}\} \in \left[ \frac{b(\beta + 1) - 2d - p_{i \rightarrow}}{2c}, \zeta + \frac{p_{i \leftarrow}}{2c} \right] \forall i \leq N \right\} \cap \mathcal{D}_{N_A, N}.$$

in finite time, and that this set is invariant under (6.2). Then, we conclude with the Lyapunov function

$$\mathbf{z} \in \mathcal{K}_{N_A, N} \mapsto \sum_{i \leq N_A} \ln \left( \frac{z_{A,i} + z_{a,i}}{z_{A,i} - z_{a,i}} \right) + \sum_{N_A < i \leq N} \ln \left( \frac{z_{a,i} + z_{A,i}}{z_{a,i} - z_{A,i}} \right).$$

As a conclusion, several generalisations are possible and a lot of assumptions can be relaxed in the initial simple model. We can also combine some of the generalisations for the needs of a particular system. However, observe that the mating preference influences the time needed to reach speciation in the same way.

#### APPENDIX A. TECHNICAL RESULTS

This section is dedicated to some technical results needed in the proofs. We first prove the convergence when  $K$  goes to infinity of the sequence of rescaled processes  $\mathbf{Z}^K$  to the solution of the dynamical system (1.6) stated in Lemma 1.1.

*Proof of Lemma 1.1.* The proof relies on a classical result of [18] (Chapter 11). Let  $\mathbf{z}$  be in  $\mathbb{N}^{\mathcal{E}}/K$ . According to (1.1)-(1.4), the rescaled birth, death and migration rates

$$(A.1) \quad \tilde{\lambda}_{\alpha,i}(\mathbf{z}) = \frac{1}{K} \lambda_{\alpha,i}(K\mathbf{z}) = \lambda_{\alpha,i}(\mathbf{z}), \quad \tilde{d}_{\alpha,i}(\mathbf{z}) = \frac{1}{K} d_{\alpha,i}^K(K\mathbf{z}) = [d + cz_{A,i} + cz_{a,i}] z_{\alpha,i},$$

and

$$\tilde{\rho}_{i \rightarrow i}(\mathbf{z}) = \frac{1}{K} \rho_{i \rightarrow i}^K(K\mathbf{z}) = \rho_{i \rightarrow i}(\mathbf{z}), \quad (\alpha, i) \in \mathcal{E}$$

are Lipschitz and bounded on every compact subset of  $\mathbb{N}^{\mathcal{E}}$ , and do not depend on the carrying capacity  $K$ . Let  $(Y_{\alpha,i}^{(\lambda)}, Y_{\alpha,i}^{(d)}, Y_{\alpha,i}^{(\rho)}, (\alpha, i) \in \mathcal{E})$  be twelve independent standard Poisson processes. From the representation of the stochastic process  $(\mathbf{N}^K(t), t \geq 0)$  in (1.5) we see that the stochastic process  $(\bar{\mathbf{Z}}^K(t), t \geq 0)$  defined by

$$\begin{aligned} \bar{\mathbf{Z}}^K(t) = \mathbf{Z}^K(0) + \sum_{(\alpha,i) \in \mathcal{E}} \frac{\mathbf{e}_{\alpha,i}}{K} \left[ Y_{\alpha,i}^{(\lambda)} \left( \int_0^t K \tilde{\lambda}_{\alpha,i}(\bar{\mathbf{Z}}^K(s)) ds \right) - Y_{\alpha,i}^{(d)} \left( \int_0^t K \tilde{d}_{\alpha,i}(\bar{\mathbf{Z}}^K(s)) ds \right) \right] \\ + \sum_{(\alpha,i) \in \mathcal{E}} \frac{(\mathbf{e}_{\alpha,i} - \mathbf{e}_{\alpha,\bar{i}})}{K} Y_{\alpha,i}^{(\rho)} \left( \int_0^t K \tilde{\rho}_{\alpha,i}(\bar{\mathbf{Z}}^K(s)) ds \right), \end{aligned}$$

has the same law as  $(\mathbf{Z}^K(t), t \geq 0)$ . Moreover, a direct application of Theorem 2.1 p 456 in [18] gives that  $(\bar{\mathbf{Z}}^K(t), t \leq T)$  converges in probability to  $(\mathbf{z}^{(\mathbf{z}^0)}(t), t \leq T)$  for the uniform norm. As a consequence,  $(\mathbf{Z}^K(t), t \leq T)$  converges in law to  $(\mathbf{z}^{(\mathbf{z}^0)}(t), t \leq T)$  for the same norm. But the convergence in law to a constant is equivalent to the convergence in probability to the same constant. The result follows.  $\square$

We now recall a well known fact on branching processes which can be found in [2] p 109.

**Lemma A.1.** • *Let  $Z = (Z_t)_{t \geq 0}$  be a birth and death process with individual birth and death rates  $b$  and  $d$ . For  $i \in \mathbb{Z}^+$ ,  $T_i = \inf\{t \geq 0, Z_t = i\}$  and  $\mathbb{P}_i$  is the law of  $Z$  when  $Z_0 = i$ . If  $d \neq b \in \mathbb{R}_+^*$ , for every  $i \in \mathbb{Z}_+$  and  $t \geq 0$ ,*

$$(A.2) \quad \mathbb{P}_i(T_0 \leq t) = \left( \frac{d(1 - e^{(d-b)t})}{b - de^{(d-b)t}} \right)^i.$$

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